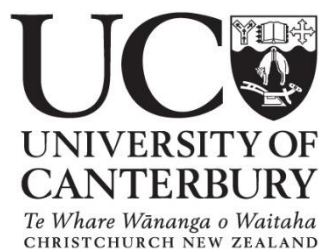

Acoustic analysis of slow click function and foraging in sperm whales (*Physeter macrocephalus*) off Kaikoura, New Zealand

By

Manuel Goulartt de Medeiros de Carvalho Fernandes

A thesis submitted in partial fulfilment of the requirements
for the Degree of Doctor of Philosophy in Zoology at the
University of Canterbury
New Zealand



December 2016

Table of contents

Table of contents	1
Abstract.....	5
Acknowledgments	7
1. General introduction	11
1.1. Sperm whale life history.....	11
1.2. Social structure and sexual segregation	12
1.3. Diet and foraging behaviour.....	14
1.4. Sperm whale acoustics	15
1.5. Kaikoura feeding ground	18
1.6. Thesis overview	19
1.7. References	20
2. A function analysis of male sperm whale slow clicks on a male-only foraging habitat.....	27
Abstract.....	27
2.1. Introduction.....	28
2.2. Methods.....	31
2.2.1. Field work.....	31
2.2.2. Acoustic hardware	33
2.2.3. Photo-identification	34
2.2.4. Acoustic data	35
2.2.5. Data extraction	35
2.2.6. Statistical analyses.....	39
2.3. Results	41
2.3.1. General patterns	41
2.3.2. Slow clicks at start of dive	46
2.3.3. Slow click events	48
2.3.4. Slow click echoes	49
2.4. Discussion	51
2.4.1. General	51
2.4.2. Slow clicks as communication	52
2.4.3. Slow clicks as echolocation	54
2.5. References	57

3. Slow click structure and its relationship to body size and directionality	61
Abstract.....	61
3.1. Introduction.....	62
3.2. Methods.....	65
3.2.1. Field work.....	65
3.2.2. Estimating body length from regular clicks.....	65
3.2.3. Estimating body length from slow clicks.....	66
3.2.4. Spectral analysis of slow clicks.....	66
3.2.5. Slow click pulse structure	68
3.2.6. Statistical analyses.....	70
3.3. Results	71
3.3.1. Estimating body length from regular clicks.....	71
3.3.2. Estimating body length from slow clicks.....	71
3.3.3. Spectral analysis of slow clicks.....	72
3.3.4. Slow click pulse structure	77
3.4. Discussion	79
3.5. References	83
4. Synchronised surfacing: codas, slow clicks and long-term bonds	89
Abstract.....	89
4.1. Introduction.....	90
4.2. Methods.....	93
4.2.1. Data collection and analysis.....	93
4.3. Results	95
4.3.1. Available data.....	95
4.3.2. Brief description of the field observation.....	95
4.3.3. Overview	97
4.3.4. Coda-creaks	98
4.3.5. Spectral frequency analysis of coda and slow clicks	98
4.3.6. 'Coda codas' and 'slow click codas'	101
4.3.7. Slow clicks and Codas	102
4.3.8. Coda matching.....	105
4.4. Discussion	106
4.4.1. General	106
4.4.2. Coda-creaks	107
4.4.3. Stereotyped patterns of clicks	108

4.4.3.1.	<i>Slow click codas (SCcodas)</i>	108
4.4.3.2.	<i>Codas</i>	109
4.4.4.	<i>Slow clicks</i>	110
4.4.5.	<i>Conclusions</i>	111
4.5.	<i>References</i>	112
5.	Relationship of bathymetry and commercial fisheries with sperm whale creaks	117
Abstract.....		117
5.1.	<i>Introduction</i>	118
5.2.	<i>Methods</i>	121
5.2.1.	<i>Field work</i>	121
5.2.2.	<i>Creak characteristics</i>	121
5.2.3.	<i>Habitat features associated with creaks</i>	124
5.2.4.	<i>Fisheries data and relationship to creaks</i>	124
5.2.5.	<i>Statistical analysis</i>	125
5.3.	<i>Results</i>	126
5.3.1.	<i>Creak characteristics</i>	126
5.3.2.	<i>Habitat features associated with creaks</i>	128
5.3.3.	<i>Fisheries data and relationship to creaks</i>	129
5.4.	<i>Discussion</i>	132
5.4.1.	<i>Creak characteristics</i>	132
5.4.2.	<i>A note on long creaks</i>	135
5.4.3.	<i>Habitat features associated with creaks</i>	137
5.4.4.	<i>Fisheries data and relationship to creaks</i>	137
5.4.5.	<i>Conclusions</i>	138
5.5.	<i>References</i>	139
6.	General discussion	145
6.1.	<i>Future research</i>	151
6.2.	<i>References</i>	153

Abstract

Sexually immature male sperm whales (*Physeter macrocephalus*) disperse from their natal areas and move to higher latitude male-only foraging grounds, such as those off New Zealand and Norway. In these areas they are found in aggregations, in which a relatively high concentration of animals congregate in a specific area. Males within aggregations continuously forage, yet seemingly dive in a solitary manner. The Kaikoura submarine canyon off New Zealand is an area where male sperm whales aggregate. This canyon is among the most productive deep sea regions in the world, and has been used for foraging both by individual male sperm whales over years, as well by transient animals which have only been seen once.

Slow clicks are vocalisations only used by males. Typically displayed in bouts with inter-click intervals of 3-9 s, they consist of low frequency (2-4 kHz) sharp clicks with a strong reverberation and apparent source levels around 201 dB_{peak} re 1 µPa at 1 m. Slow clicks have much lower directionality than regular echolocating clicks, resulting in their characteristic strong and lasting seafloor echo. At breeding grounds, slow clicks seem to be displayed in long sequences while males are close to, or at the surface, and these have been suggested to function as vocal display used in competition and/or to attract females. In contrast, at male-only foraging grounds, slow clicks are heard in shorter sequences at the end of foraging dives (and also, at times, during surfacing), with these being heard in almost half of all foraging dives recorded in this study. The diving-phase pattern associated with slow clicks appears consistent across male aggregations recorded here, off Kaikoura, and those found off Norway¹. While the function of slow clicks is still unclear, the different social and slow-clicking patterns observed suggests a context-dependent function in communication.

I used a towed hydrophone array and photo-identification data from individually-tracked whales during complete foraging dives to further understand the function of slow clicks in the Kaikoura foraging ground. I investigated the presence and number of slow clicks as a function of other acoustically-detected whales in the area, which indicated an increased rate of slow clicking with increasing number of 'neighbours'. I examined slow click structure, including centre frequency, waveform, and, as body size-related information is encoded in regular echolocating clicks, the occurrence of multiple pulses within clicks, to examine the relationship between this vocalisation and body length. The centre frequency of slow clicks differed between individuals and their waveform revealed a multi-pulsed structure in seventy percent of clicks analysed. However, neither the inter-pulse interval (time between pulses within a click) of slow clicks, nor their centre frequency, correlated with body size. Additionally, the

analysis of the pulse structure and amplitude of slow clicks within bouts suggests that slow clicks display a broad but somewhat defined directionality, which may allow slow clicking whales to target goals by adjusting their body posture. Additionally, I explored the use of slow clicks and codas, which are stereotyped patterns of clicks used for communication, produced by a pair of males synchronising their surfacing time and dives. Over a complete dive cycle and surfacing time I examined the spectral characteristics and waveform of codas (click sequences) and slow clicks, as well as coda duration. Codas made using clicks with spectral and waveform characteristics of slow clicks were termed “slow click codas”. These were longer, and showed lower centre frequency and higher relative amplitude than traditional codas and may suggest some form of communication between whales in synchrony. Finally, I looked at the feeding vocalisation (creak) rate, duration, and the relationship between creak presence, bathymetry and the commercial fisheries within the underwater canyon off Kaikoura as a proxy for areas with an abundance for potential prey. Results suggest that males in this area may be targeting fewer but larger and/or more nutritious prey (i.e. fewer but longer creaks) compared to other studied areas.

In conclusion, the diving phase-related use of slow clicks, their acoustic properties, including the centre frequency and waveform related information, coupled with the field observations analysed and the history of male bachelor group composition, suggests that slow clicks may function as a contact call, which could be used for individual and/or group recognition.

1- Oliveira, C., M. Wahlberg, M. Johnson, P. J. O. Miller, and P. T. Madsen. 2013. The function of male sperm whale slow clicks in a high latitude habitat: communication, echolocation, or prey debilitation? *Journal of the Acoustical Society of America* 133(5):3135-3144.

Acknowledgments

I would like first to thank my supervisor, the Associate Professor Ximena Nelson, for having accepted me as a student and for the glove-fitting like approach to my “student condition”. Thank you, Ximena, I am grateful for having been supervised by you, technically and personally. I would like to thank Larry Field for introducing me to many aspects of the world of acoustics, and for supervising me while I was conducting field work in Kaikoura. Your natural enthusiasm matched my own, boosting it even further, and that helped me.

I also want to highlight, and appreciate, the opportunity provided by Tim Markowitz, Jonathan Gordon and Christopher Richter, to engage in their New Zealand Department of Conservation (DOC) project which led to my field data collection. Jonathan and Tim also offered support and advice in the early stages of this journey. Thank you to the University of Canterbury (UC) field stations manager Jack Van Berkel, who also guided me through the process of becoming a UC PhD student and to the UC postgraduate office for being understanding of the many instances in which I had to ‘suspend’ my work for weeks or months at a time. Since field work was completed through a DOC-funded project, I would like to thank DOC for the logistic and financial support provided. In particular, I thank Mike Morrissey for training the research team in safety and boat operations in general, and for setting up and maintaining the DOC research vessel “Titi” during field work. Mike was also our skipper at times, thank you.

I thank Saana Isojunno for her contribution to the experimental design of the field work, and for helping to collect some of the data used in my thesis. Thank you also for sharing your super-hero like skills when I most needed them, as well as for your comments and advice. Thank you Brian Miller for providing detailed instructions for the Pamguard sperm whale IPI plug-in you developed; for your time, and patience answering all my questions. I would also like to thank Alex James and Daniel Gerhard from the UC Department of Mathematics and Statistics for help with my analysis in Chapters 2 and 5, and to Miranda van der Linde for proving photo-identification data used in Chapter 4.

I am also very grateful to the over 56 volunteers that were part of the field work team, including: Alicia Sanchez, Ben Williams, Bryony Manley, Cally Meredith, Cécile Houle, Chanyo Bunpunloot, Claire Giner, Claire Hallier, Courtney Wilson, Daniel Lindner, Dean Harliwich, Elena Trentin, Emily, Emma Ball, Eriko Fukuda, Fergus Grant, Gemma Veneruso, Hannah Curtis, Heather Vance, Helen Fairlamb, Isabelle Sikora, James Miles, Jason Gayton, Jean-Mathias Jourdier, Jenipher Cate, Jessica Riggan, John Hackett, Kalliopi Ghikopoulou,

Kate Sprogis, Katie-Anne Isabella, Kerry Froud, Kirsty Everley, Adrien Lambrechts, Leila Fouda, Lindsey Nielsen, Lorna Deppe, Nasman, Ophelie Sagnol, Pete Weiner, Rémi Bigonneau, Rose Thorogood, Ruben Venegas, Saana Isojunno, Sandra Nussbaum, Sanja Heikkila, Sara Anderson, Sarah Barry, Sarah Jackson, Sibilski Lise, Sol Heber, Stephanie Czudaj, Sue Jackson, Tay Shu Hui Petrina, Tom Robinson, Tom Barnfield and Vall Lubrick. Their presence and skills were fundamental for the collection of the data. I also want to thank Ophelie Sagnol for helping with organising volunteers throughout the seasons of field work.

I would also like to thank all the research vessel sippers involved in data collection trips: Henry Nee, Hank Posa, Pete Busher, Grant Kannedy, Mike Morrissey, Rex Kahu and Roger Williams. Our main master, however, was Henry Nee (who passed away after the field work finished). I am grateful and honoured to have had the opportunity to work with, and learn from, such a legendary seadog with extensive experience and good practice. Henry, and Valery (Henry's wife) were my neighbours and we became friends, which was a personal highlight during my Kaikoura times.

It was great to cooperate with managers and staff of Kaikoura Helicopters, Whale Watch Kaikoura, Air Kaikoura and Wings Over Whale, who were all directly involved in the field work in different ways, including data collection. I truly appreciated the positive and cooperative attitude in the field, and appreciated the local knowledge sharing with our team.

I would like to thank Cláudia Faustino, Frederico Oliveira and Inês Paixão for their comments on some of my chapters, and Luis Bentes for taking the time to help with GIS software.

I am grateful to the Ministry of Primary Industries, specifically to Paul Berentson, who organised and provided the commercial and recreational fisheries data (Deed Number CAN2015-001) for Chapter 5. The National Institute of Water and Atmosphere Research provided the high resolution bathymetry map of the Kaikoura canyon.

This PhD was a challenge I embraced with passion, and the only prior objective was to further learn, in a scientific manner, about sperm whales, while enjoying life. It was during this journey that I met Sol Heber, my partner. Thanks to her, we now have two additional human beings at home, Luca and Manu. They represent the start of our "human family unit" which I embrace with love and commitment. Thank you, Sol, for adjusting your life in favour of this personal goal of mine, for supporting me every day, and for your expert help throughout.

Last but not least, I want to thank my extraordinary mother and my father, but also my extended family and friends. Thank you for your guidance, unconditional support, and freedom

to follow my path, while always being there for me. You are all responsible for my achievements and I am very grateful for that.

1. General introduction

1.1. *Sperm whale life history*

The sperm whale, or cachalot (*Physeter macrocephalus*) is the largest of the toothed whales (odontocetes) and is a deep-diving cetacean that can be found in all the world's oceans (Whitehead 2003) (Figure 1.1). These whales have a lifetime comparable to that of humans and are strongly sexually dimorphic, with adult males being about a third longer and three times heavier than adult females. They exhibit a complex social structure which also varies depending on sex, with adult males and females living apart (Rice 1989, Whitehead 2003).

Males achieve puberty at the age of 7-11 years, when they measure 9-10 m, and reach sexual maturity at 18-21 years, when they measure approximately 13 m. However, physical maturity is only reached between 35-60 years of age, when they measure about 16-18 m (Rice 1989). According to Bennett (1840), the largest reported male was about 23 m long; however, most large males killed by whalers did not exceed 18 m, weighing about 60 metric tons (Bennett 1840, Clarke 1956, Ohsumi 1966). In contrast, large females reach just over 12 m long and weigh approximately 20 metric tons (Clarke 1956, Lockyer 1976, Best 1979). Females first conceive at about nine years of age, giving birth to a four meter calf every 4-6 years (Best et al. 1984, Rice 1989) until their late twenties, when the birth rate drops considerably (Best et al. 1984). Calves start ingesting solid food at about one year of age and suckle until they are about two years old, although milk has been found in the stomachs of animals as old as 13 years (Best et al. 1984).

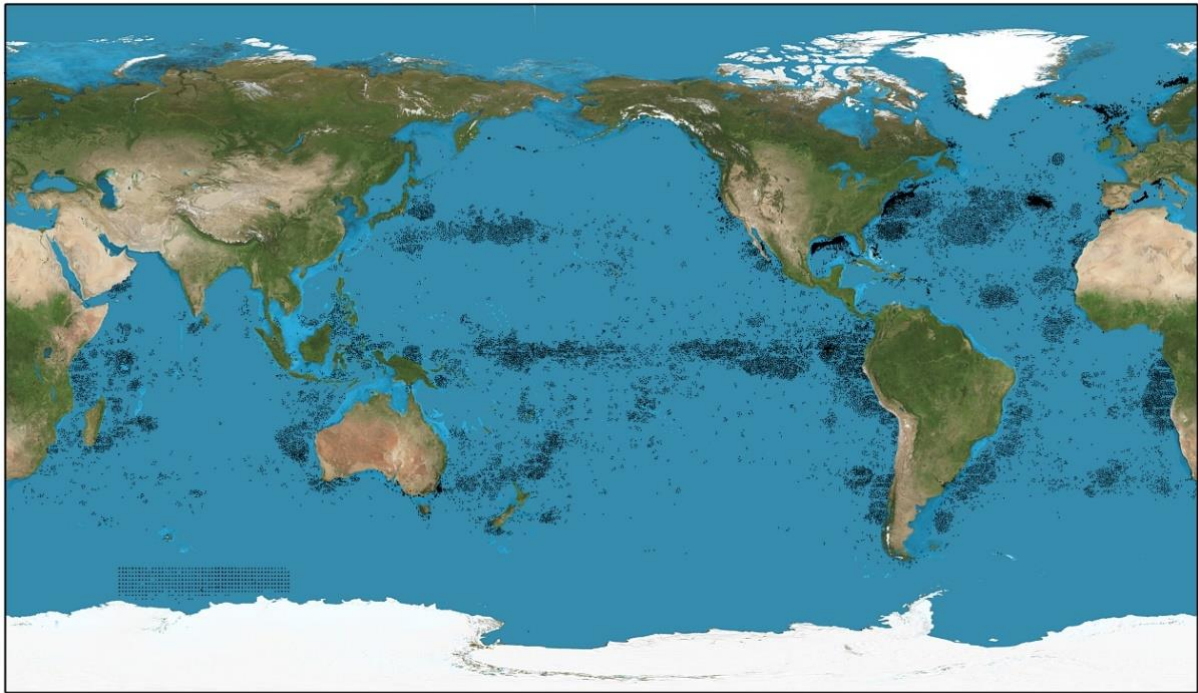


Figure 1.1 – Distribution of sperm whales (black dots) based on records of whalers and surveyors around the world (Wikipedia 2013).

1.2. Social structure and sexual segregation

Females with calves and immature offspring live in matrilineal social systems and are mostly found in temperate and tropical waters generally delimited by 40° of latitude North and South of the equator (Whitehead 2003). In the Pacific Ocean, however, females are reported as far as 59° North (Ivashchenko et al. 2014) and South (Ivanov (1972), cited in Best (1979)).

The basic unit of female social organisation is the ‘family unit’, or ‘social unit’. A family unit is composed of one or more matrilineal lines that form stable relationships for decades (Richard et al. 1996, Gero et al. 2014). Units temporarily associate in ‘groups’ (Whitehead et al. 1991, Whitehead 2003), which have occasionally been reported as ‘body of whales’, where countless animals spread over several miles (Bennett 1840, Clarke 1956). In the North Atlantic, females show philopatry within their home range (Engelhaupt et al. 2009), frequently moving distances up to 2000 km, and occasionally twice that (Whitehead et al. 2008). In the North Pacific, however, whaling and marking data suggest more erratic movements (Mizroch and Rice 2013).

The driving force responsible for long-term associations between females is thought to be related to alloparental care (Whitehead 1996), including reducing predation risk (Best 1979, Gordon 1987, Pitman et al. 2001). Family units alternate foraging phases with long periods ‘socialising’ at the surface in close proximity to each other (Best 1979 Whitehead and Weilgart

1991, Watwood et al. 2006), during which the whales rest, travel and/or interact. It is mostly during this period that social behaviours, including bonding vocalisations, occur (Whitehead and Weilgart 1991, Weilgart and Whitehead 1993).

In contrast, males leave their natal family units during puberty, at about nine years of age (Ohsumi 1971, Mendes et al. 2007). This separation, which includes dispersing towards higher latitudes, is believed to be due to demand for nutritional requirements needed to achieve physical maturity to become competitive when returning to lower latitude breeding grounds (Best 1979, Teloni et al. 2008, Steiner et al. 2012). The distribution of males reaches the edges of the polar pack but may also overlap with that of females at lower latitudes (Best 1979, Rice 1989, Whitehead 2003). The social life and movement patterns of males after dispersal are very unclear (Lettevall et al. 2002), but are distinctly different from those of females, which have been consistently reported following the same general patterns, i.e., socializing periods alternating with foraging on a daily basis (Whitehead 2003). There is a paucity of data on the periodicity of the return of males to breeding grounds in subsequent breeding migrations, and we don't know whether they return to the same foraging grounds between breeding seasons (Whitehead 2003). While there is some evidence of seasonality in the presence of mature males at low latitudes, which roughly coincides with the breeding season (Whitehead 2003), large males have also been reported as present throughout the year in the Galápagos islands (Hope and Whitehead 1991), the Azores archipelago (Clarke 1956), and off breeding grounds near Chile (Whitehead 2003). Male movements are much greater than those of females; there are records of males that have crossed oceans and the equator (Mitchell (1975) and Ivashin (1967), both cited in Whitehead (2003)) and genetic and marking data also show they change ocean basins (Brown 1981, Lyrholm et al. 1999).

Dispersing males tend to associate in groups according to their sexual development stage (Gaskin 1970). These groups, referred to as 'bachelor groups', are generally composed of animals of the same age and size and tend to be composed of fewer animals as individuals grow larger (Clarke 1956, Gaskin 1970, Ohsumi 1971, Best 1979). Nevertheless, there is no evidence of long-term bonds between males (Lettevall et al. 2002), and physically mature males are often referred to as 'solitary' animals when observed surfacing, regardless of the presence of other whales of the same social status (i.e., of similar age and size) within a mile (Clarke 1956, Gaskin 1970, Best 1979). Comparable to the socialising behaviour observed in females, male bachelor groups have been observed in 'tight schools' off the Azores islands (central North Atlantic) and in New Zealand (Clarke 1956, Gaskin 1970). In some cases these males frequently split and re-join (Best 1979). These behaviours seem to be associated with

sexually - but not physically - mature animals (Caldwell et al. 1966, Best 1979). At high latitudes males are often found in ‘aggregations’, a term used to describe concentrations of males spanning up to roughly 30 km (Best 1979, Whitehead et al. 1992, Jaquet et al. 2000), but whether this happens exclusively due to patchy food distribution, or if there are additional mutual benefits, is not clear (Lettevall et al. 2002). Male aggregations, however, have been observed moving consistently together. Males off the Galápagos islands (Christal and Whitehead 1997) and California (Caldwell et al. 1966) have been tracked using coordinated movements for distances of up to 50 km. The ability to maintain contact and/or coordinate may play an important role for foraging or migrating males (Best et al. 1984, Rice 1989). Off the Azores islands (a female feeding and breeding ground), males seem to consistently show up in synchrony, and on one occasion, 16 large males were found (and registered) aligned in a parallel formation before diving in synchrony (personal observation). If dispersing males actively keep track of other males, how this relates to their survival or reproductive success are questions that have not yet been resolved.

1.3. *Diet and foraging behaviour*

The bulk of the diet of sperm whales in most of the world’s oceans consists of mesopelagic and bathypelagic cephalopods (Clarke 1956, Clarke 1980, Best 1999). However, off New Zealand, Iceland and Antarctica, fish are an important source of food (Gaskin and Cawthorn 1967, Martin and Clarke 1986, Clarke et al. 1993, Clarke 1996). Foraging sperm whales typically dive for about 40 min and recover at the surface for approximately 8 min (Gordon et al. 1992, Gordon and Steiner 1992). This behaviour accounts for their main activity on a daily basis (Arnbom and Whitehead 1989, Jaquet et al. 2000).

There are a number of differences between males and females with respect to foraging. While females are known to feed at a restricted range of depths (mesopelagic and bathypelagic), up to about 2000 m (Caldwell et al. 1966, Watkins et al. 2002, Amano and Yoshioka 2003, Nosal and Frazer 2006), males forage over a wider range of depths, from the surface down to the seafloor (Miller et al. 2013a). These differences are reflected both in their stomach contents (Clarke et al. 1993, Best 1999), and in vocalizations related to foraging (Miller et al. 2004, Teloni et al. 2008). Males also consume larger and more diverse prey than females (Clarke 1956, Clarke 1980). Females spend several hours daily at the surface (Whitehead 2003, Watwood et al. 2006), and tend to be found further offshore, away from the continental shelf, whereas males at higher latitudes seem to forage continuously, rarely take a

break (Gordon et al. 1992, Jaquet et al. 2000, Teloni et al. 2008), and show a preference for continental slopes and submarine canyons (Best 1999, Whitehead 2003).

1.4. *Sperm whale acoustics*

Odontocetes use click sounds as a bio-sonar, or echolocation. These clicks are particularly useful to perceive the environment outside their visual range, and assist the animal to locate prey, conspecifics, and predators, as well as to navigate (Thomas et al. 2004). Echolocation is possible through a complex sound apparatus, which in essence involves two organs: the phonic lips and the melon. The phonic lips are responsible for the production of the sound pulse, due to forcing pressurised air in the nasal complex through these vibratory structures. The melon is a waxy organ next to the phonic lips that works as an acoustic directional lens (Au and Simmons 2007). When compared to other odontocetes, the size and complexity of the melon in sperm whales is extreme (Norris and Harvey 1972). Indeed, sperm whales own the largest sound generator of all animals (up to one third of the whale's length), which is responsible for the highest recorded sound pressure levels of any biological source (236 dB re: 1 μ Pa (rms); (Cranford 1999, Møhl 2004). Additionally, clicks produced by sperm whales differ from those of all other echolocators, exhibiting a peculiar multi-pulsed structure (Backus and Schevill 1966) (Figure 1.2) and researchers are still learning about the relationship between the structure of the melon and the resulting properties of click vocalisations (Huggenberger et al. 2016).

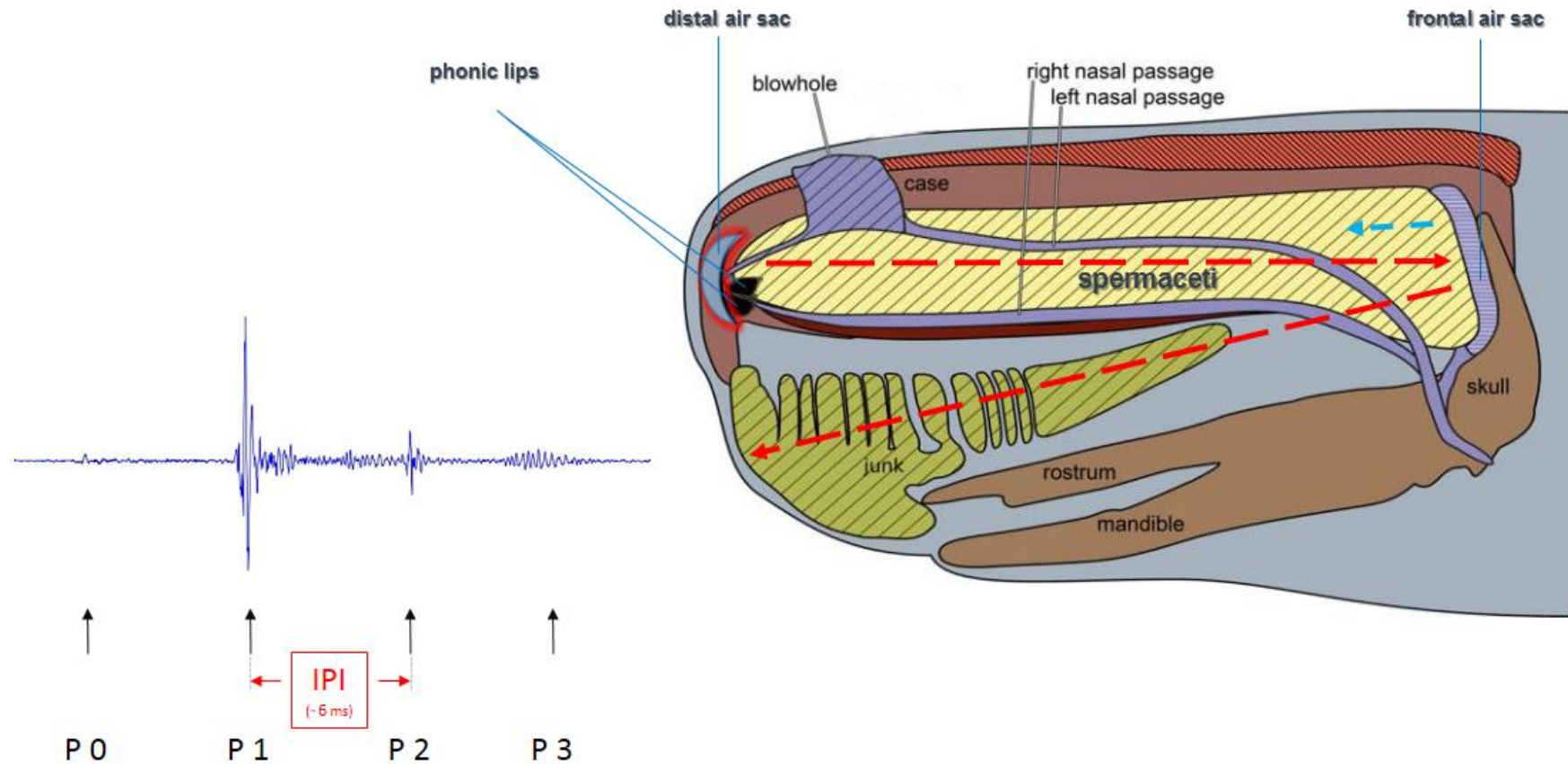


Figure 1.2 – Left lateral view of the anatomical structures of the head of an adult sperm whale (dorsal side up). Red dashed arrows indicate the assumed sound path from the initial sound pulse, P0, originating from the phonic lips, which resonates on the distal sac to be directed backwards to the frontal sac through the spermaceti organ, in yellow, and forward and out through the junk, in green. Part of the reflected energy bounces back and forth through the spermaceti (blue dashed small arrow), accounting for the pulsed structure of the clicks. Based on bent acoustic horn hypothesis (Møhl 2001). P0 - P3 correspond to the different pulses within a quasi on-axis regular click recorded in this study. The inter-pulse interval (IPI) represents the two-way travel time between the reflecting distal and frontal air sacs (Modified from Huggenberger et al. (2016).

Norris and Harvey (1972) proposed a model to explain the multi-pulsed nature of sperm whale clicks, where the initial sound pulse, P0, is produced pneumatically in the phonic lips which are connected to an adjacent air filled cavity, the distal sac (Figure 1.2). The resonating distal sac directs most energy backwards through the oil-filled spermaceti organ until it is reflected forward by another air filled structure (frontal sac) through the junk (Cranford 1999, Møhl et al. 2003), and finally radiated into the water (Figure 1.2). The junk thus functions as an acoustic lens directing the outgoing pulse (P1) in a directional beam (Møhl et al. 2003, Zimmer et al. 2005). Additional pulses (i.e., P2 and P3), which show an exponentially decaying amplitude, result from part of the forward-reflected energy from the P1 pulse bouncing between the two air sacs (blue dashed small arrow in Figure 1.2). The time difference between pulses within clicks represents the two-way travel time between the reflecting frontal and distal air sacs (Norris and Harvey 1972) and is thus related to the length of the spermaceti chamber (Adler-Fenchel 1980), which, in turn, relates to the total size of the animal (Nishiwaki et al. 1963). This relationship allows the estimation of the total body length of individuals (Møhl et al. 1981, Gordon 1991).

Sperm whales produce a variety of sounds, the most common of which are clicks, with different click types serving different functions (Gordon 1987, Goold 1999, Weir et al. 2007). ‘Regular’, or ‘usual’ clicks are the most frequent. These powerful clicks are usually heard at regular intervals of 0.5-2 s and function for long-range directional echolocation used to find individual prey, or prey patches, while additionally providing information for navigation (Møhl et al. 2000, Jaquet et al. 2001, André et al. 2007). When homing in on their prey just prior to capture, sperm whales switch from regular to ‘creak’ clicks (or ‘buzzes’). Although they contain less power than regular clicks, creaks also show high directionality (Madsen et al. 2002b) and may be heard at rates of up to ninety clicks per second (Jaquet et al. 2001). Creak rates are used as an indicator of foraging success (Gordon 1987, Miller et al. 2004) and their duration likely relates to the quality of the prey (Teloni et al. 2008). ‘Codos’ are stereotyped patterns of clicks used mostly by adult females within social units, during socializing periods (Whitehead and Weilgart 1991, Marcoux et al. 2006). However, codas have also been associated with the start and end of foraging dives, both within family units (Watkins and Schevill 1977, Madsen et al. 2002a), and in male bachelor groups in the Mediterranean Sea (Frantzis and Alexiadou 2008). Codas vary geographically and have been referred to as ‘dialects’, part of a non-human culture (Rendell and Whitehead 2001) identified as ‘vocal clans’, which results in units preferring to associate with other units of their own acoustic clan (Rendell and Whitehead 2003). Codas are thought to be transmitted vertically through

generations (Rendell and Whitehead 2003). Finally, ‘slow clicks’ are a click type known only from males, both at low latitude breeding grounds (Weilgart and Whitehead 1988, Whitehead 1993), and at higher latitude male-only foraging grounds (Oliveira et al. 2013). As most slow clicks are heard in bouts with long inter-click intervals of 4-10 s towards the end of foraging dives, or are heard at the surface (Jaquet et al. 2001, Oliveira et al. 2013), slow clicks are generally associated with foraging. Yet, based on their spectral frequency characteristics, low directionality and dive phase in which they mostly occur, the function of slow clicks has been proposed as a form of communication (Madsen et al. 2002b, Oliveira et al. 2013). In breeding areas this function is attributed to vocal display in competition for females (Gordon 1987, Weilgart and Whitehead 1988). In male-only areas at higher latitudes, the communication function is attributed to acoustic display in competition for food, or practicing courtship displays before migrating to breeding grounds (Mullins et al. 1988, Madsen et al. 2002b). Highlighting how little we understand slow clicks, other proposed functions include their use as a form of wide-range echolocation (Gordon 1987, Mullins et al. 1988, Goold 1999, Tyack and Clark 2000, Jaquet et al. 2001), or to maintain cohesion among dispersing males (Christal and Whitehead 1997).

1.5. *Kaikoura feeding ground*

The Kaikoura submarine canyon, off the East coast of the South Island of New Zealand, is a feeding ground for male sperm whales and is an exceptional location for research, since animals can reliably be found year-round within a few nautical miles from shore. Due to the relative ease with which they can be studied, a number of studies since the early nineteen nineties have contributed to a better understanding of their distribution, abundance, population structure, diving and vocal behaviour, and individual growth rates, as well as monitoring responses to human interactions (Gordon et al. 1992, Dawson et al. 1994, Childerhouse et al. 1995, Jaquet et al. 2000, Jaquet et al. 2001, Lettevall et al. 2002, Richter et al. 2003, Richter et al. 2006, Growcott et al. 2011, Markowitz et al. 2011, Miller et al. 2013a, Miller et al. 2013b, Sagnol et al. 2014).

The Kaikoura canyon holds a stable male aggregation, with abundance estimates suggesting up to 100 whales using the area in one season (Childerhouse et al. 1995, Van der Linde 2010), or anywhere from four (Sagnol et al. 2015) to 14 (Lettevall et al. 2002) whales present at any given time. The whales found here are predominantly foraging (Jaquet et al.

2000) and there is no confirmation, based on visual observation, of any social organisation among males in the area (Lettevall et al. 2002).

1.6. *Thesis overview*

The data used for this research were collected during a New Zealand Department of Conservation project to assess the effects of whale watching activity on the acoustic and surface behaviour of sperm whales in the Kaikoura canyon (Markowitz et al. 2011).

This thesis focuses on the acoustic behaviour of sperm whales in this male-only ground, in particular concerning slow clicks. Specifically, in Chapter 2, I tested whether the number of other sperm whales in the area affected the number of slow clicks and the slow click bouts produced by the focal whale, and investigated the potential for slow clicks to function as echolocation of large targets, including the seafloor. The spectral and structural characteristics of slow clicks were analysed in detail in Chapters 3 and 4. In Chapter 3, I analysed the structure of slow clicks in terms of centre frequency and occurrence of multiple pulses. Specifically, I tested the relationship between the central frequency of slow clicks and the estimated size of individuals, which were calculated from measurements of the inter-pulse intervals of their regular clicks. A selection of those slow clicks displaying a multi-pulse structure was used to test if these were related to the size of the whale, as is the case for regular clicks (Adler-Fenchel 1980, Growcott et al. 2011). In Chapter 4, I describe a rare observation of physical and vocal interaction between two males, which coordinated at the surface and produced codas, slow clicks and coda-creaks (fast series of clicks associated with socialising females). In Chapter 5, I investigated creak rates and duration by looking at its relationship with bathymetry and to the areas of local commercial fisheries. Chapter 5 gives a foraging context for the previous chapters, which focus on slow clicks. Finally, I briefly discuss my main findings in a general discussion (Chapter 6).

1.7. References

- Adler-Fenchel, H. S. 1980. Acoustically derived estimate of the size distribution for a sample of sperm whales (*Physeter catodon*) in the Western North Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* **37**(12):2358-2361.
- Amano, M., and M. Yoshioka. 2003. Sperm whale diving behavior monitored using a suction-cup-attached TDR tag. *Marine Ecology Progress Series* **258**:291-295.
- André, M., T. Johansson, E. Delory, and M. Van der Schaar. 2007. Foraging on squid: the sperm whale mid-range sonar. *Journal of the Marine Biological Association of the UK* **87**(1):59-67.
- Arnbom, T., and H. Whitehead. 1989. Observations on the composition and behaviour of groups of female sperm whales near the Galápagos Islands. *Canadian Journal of Zoology* **67**(1):1-7.
- Au, W. W. L., and J. A. Simmons. 2007. Echolocation in dolphins and bats. *Physics Today* **60**(9):40-45.
- Backus, R. H., and W. E. Schevill. 1966. *Physeter* clicks. Pages 510–528 in K. S. Norris, editor. *Whales, dolphins, and porpoises*. University of California Press, Berkeley.
- Bennett, F. D. 1840. Narrative of a whaling voyage round the globe, from the year 1833 to 1836. Richard Bentley, London.
- Best, P. B. 1979. Social organization in sperm whales, *Physeter macrocephalus*. Pages 227-289 in H. E. Winn and B. L. Olla, editors. *Behavior of Marine Animals*. Springer US.
- Best, P. B. 1999. Food and feeding of sperm whales *Physeter macrocephalus* off the west coast of South Africa. *South African Journal of Marine Science* **21**(1):393-413.
- Best, P. B., P. A. S. Canham, and N. MacLeod. 1984. Patterns of reproduction in sperm whales, *Physeter macrocephalus*. *Report of the International Whaling Commission* **6**:51-79.
- Brown, S. 1981. Movements of marked sperm whales in the Southern Hemisphere. *Report of the International Whaling Commission* **31**:835-837.
- Caldwell, D. K., M. C. Caldwell, and D. W. Rice. 1966. Behavior of the sperm whale *Physeter catodon* L. Pages 677–717 in K. S. Norris, editor. *Whales, dolphins and porpoises*. University of California Press, Berkeley.
- Childerhouse, S. J., S. M. Dawson, and E. Slooten. 1995. Abundance and seasonal residence of sperm whales at Kaikoura, New Zealand. *Canadian Journal of Zoology* **73**(4):723-731.
- Christal, J., and H. Whitehead. 1997. Aggregations of mature male sperm whales on the Galápagos Islands breeding ground. *Marine Mammal Science* **13**(1):59-69.
- Clarke, M. R. 1980. Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. University of California Press, Berkeley, 324 pp.
- Clarke, M. R. 1996. Cephalopods as prey. III. Cetaceans. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **351**(1343):1053-1065.

- Clarke, M. R., H. R. Martins, and P. Pascoe. 1993. The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. Philosophical Transactions of the Royal Society of London B: Biological Sciences **339**(1287):67-82.
- Clarke, R. 1956. Sperm whales of the Azores. Discovery Reports XXVIII:237-298.
- Cranford, T. W. 1999. The sperm whale's nose: sexual selection on a grand scale? Marine Mammal Science **15**(4):1133-1157.
- Dawson, S. M., E. Slooten, and O. Jake. 1994. Distribution, abundance and population structure of sperm whales at Kaikoura. WWF-NZ, Wellington.
- Engelhaupt, D., A. R. Hoelzel, C. Nicholson, A. Frantzis, S. Mesnick, S. Gero, H. Whitehead, L. Rendell, P. J. O. Miller, and R. De Stefanis. 2009. Female philopatry in coastal basins and male dispersion across the North Atlantic in a highly mobile marine species, the sperm whale (*Physeter macrocephalus*). Molecular Ecology **18**(20):4193-4205.
- Frantzis, A., and P. Alexiadou. 2008. Male sperm whale (*Physeter macrocephalus*) coda production and coda-type usage depend on the presence of conspecifics and the behavioural context. Canadian Journal of Zoology **86**(1):62-75.
- Gaskin, D. E. 1970. Composition of schools of sperm whales *Physeter catodon* Linn. east of New Zealand. New Zealand Journal of Marine and Freshwater Research **4**(4):456-471.
- Gaskin, D. E., and M. W. Cawthorn. 1967. Diet and feeding habits of the sperm whale (*Physeter catodon* L.) in the Cook Strait region of New Zealand. New Zealand Journal of Marine and Freshwater Research **1**(2):156-179.
- Gero, S., M. Milligan, C. Rinaldi, P. Francis, J. C. D. Gordon, C. Carlson, A. Steffen, P. L. Tyack, P. Evans, and H. Whitehead. 2014. Behavior and social structure of the sperm whales of Dominica, West Indies. Marine Mammal Science **30**(3):905-922.
- Goold, J. C. 1999. Behavioural and acoustic observations of sperm whales in Scapa Flow, Orkney Islands. Journal of the Marine Biological Association of the UK **79**(3):541-550.
- Gordon, J. C. D. 1987. Sperm whale groups and social behaviour observed off Sri Lanka. PhD thesis. University of Cambridge, Cambridge, England.
- Gordon, J. C. D. 1991. Evaluation of a method for determining the length of sperm whales (*Physeter catodon*) from their vocalizations. Journal of Zoology **224**(2):301-314.
- Gordon, J. C. D., R. Leaper, F. G. Hartley, and O. Chappell. 1992. Effects of whale-watching vessels on the surface and underwater acoustic behaviour of sperm whales off Kaikoura, New Zealand. Department of Conservation. Science & Research Series No. 52, 35 pp.
- Gordon, J. C. D., and L. Steiner. 1992. Ventilation and dive patterns in sperm whales, *Physeter macrocephalus*, in the Azores. Reports of the International Whaling Commission **42**:561-565.
- Growcott, A., B. Miller, P. Sirguy, E. Slooten, and S. Dawson. 2011. Measuring body length of male sperm whales from their clicks: the relationship between inter-pulse intervals and photogrammetrically measured lengths. Journal of the Acoustical Society of America **130**(1):568-573.

- Hope, P. L., and H. Whitehead. 1991. Sperm whales off the Galápagos Islands from 1830-50 and comparisons with modern studies. Report of the International Whaling Commission **41**:273-286.
- Huggenberger, S., M. André, and H. H. A. Oelschläger. 2016. The nose of the sperm whale: overviews of functional design, structural homologies and evolution. Journal of the Marine Biological Association of the UK **96**(4):783-806.
- Ivanov, A. P. 1972. Small sperm whales in the Antarctic. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. **90**:182-183.
- Ivashchenko, Y. V., R. L. Brownell Jr., and P. J. Clapham. 2014. Distribution of Soviet catches of sperm whales *Physeter macrocephalus* in the North Pacific. Endangered Species Research **25**(3):249-263.
- Ivashin, M. V. 1967. Whale globe-trotter. Priroda (Moscow) **8**:105-107.
- Jaquet, N., S. Dawson, and L. Douglas. 2001. Vocal behaviour of male sperm whales: why do they click? Journal of the Acoustical Society of America **109**(5):2254-2259.
- Jaquet, N., S. Dawson, and E. Slooten. 2000. Seasonal distribution and diving behaviour of male sperm whales off Kaikoura: foraging implications. Canadian Journal of Zoology **78**(3):407-419.
- Lettevall, E., C. Richter, N. Jaquet, E. Slooten, S. Dawson, H. Whitehead, J. Christal, and P. M. Howard. 2002. Social structure and residency in aggregations of male sperm whales. Canadian Journal of Zoology **80**(7):1189-1196.
- Lockyer, C. 1976. Body weights of some species of large whales. ICES Journal of Marine Science **36**(3):259-273.
- Lyrholm, T., L. Olof, B. Johanneson, and U. Gyllensten. 1999. Sex-biased dispersal in sperm whales: contrasting mitochondrial and nuclear genetic structure of global populations. Proceedings of the Royal Society of London B: Biological Sciences **266**(1417):347-354.
- Madsen, P. T., R. Payne, N. U. Kristiansen, M. Wahlberg, I. Kerr, and B. Møhl. 2002a. Sperm whale sound production studied with ultrasound time/depth-recording tags. Journal of Experimental Biology **205**(Pt13):1899-1906.
- Madsen, P. T., M. Wahlberg, and B. Møhl. 2002b. Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and communication. Behavioral Ecology and Sociobiology **53**(1):31-41.
- Marcoux, M., H. Whitehead, and L. Rendell. 2006. Coda vocalizations recorded in breeding areas are almost entirely produced by mature female sperm whales (*Physeter macrocephalus*). Canadian Journal of Zoology **84**(4):609-614.
- Markowitz, T. M., C. F. Richter, and J. C. D. Gordon. 2011. Effects of tourism on the behaviour of sperm whales inhabiting the Kaikoura Canyon. Report submitted to the New Zealand Department of Conservation by PACE-NZRP, Kaikoura Sperm Whale and Tourism Research Project, 20 December 2011, 121 pp.
- Martin, A. R., and M. R. Clarke. 1986. The diet of sperm whales (*Physeter macrocephalus*) captured between Iceland and Greenland. Journal of the Marine Biological Association of the UK **66**(4):779-790.

- Mendes, S., N. Jason, R. J. Reid, A. F. Zuur, and G. J. Pierce. 2007. Stable carbon and nitrogen isotope ratio profiling of sperm whale teeth reveals ontogenetic movements and trophic ecology. *Oecologia* **151**(4):605-615.
- Miller, B. S., S. Dawson, and R. Vennell. 2013a. Underwater behavior of sperm whales off Kaikoura, New Zealand, as revealed by a three-dimensional hydrophone array. *Journal of the Acoustical Society of America* **134**(4):2690-2700.
- Miller, B. S., A. Growcott, E. Slooten, and S. M. Dawson. 2013b. Acoustically derived growth rates of sperm whales (*Physeter macrocephalus*) in Kaikoura, New Zealand. *Journal of the Acoustical Society of America* **134**(3):2438-2445.
- Miller, P. J. O., M. P. Johnson, and P. L. Tyack. 2004. Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. *Proceedings of the Royal Society of London B: Biological Sciences* **271**(1554):2239-2247.
- Mitchell, E. 1975. Preliminary report on Nova Scotian fishery for sperm whales (*Physeter catodon*). *Reports of the International Whaling Commission* **25**:226-235.
- Mizroch, S. A., and D. W. Rice. 2013. Ocean nomads: distribution and movements of sperm whales in the North Pacific shown by whaling data and discovery marks. *Marine Mammal Science* **29**(2):E136-E165.
- Møhl, B. 2001. Sound transmission in the nose of the sperm whale *Physeter catodon*. A post mortem study. *Journal of Comparative Physiology A* **187**(5):335-340.
- Møhl, B. 2004. Sperm whale sonar rivals tactical sonar with source levels at 235 dB. Pages 41-42 in P. G. H. Evan and L. A. Miller, editors. *Proceedings of the workshop on active sonar and cetaceans*. European Cetacean Society Newsletter No. 42.
- Møhl, B., E. Larsen, and M. Amundin. 1981. Sperm whale size determination: outlines of an acoustic approach. Pages 327-331 in *Mammals in the Seas*. Vol. 3: General papers and large cetaceans. FAO Fisheries Series No. 5.
- Møhl, B., M. Wahlberg, P. T. Madsen, A. Heerfordt, and A. Lund. 2003. The monopulsed nature of sperm whale clicks. *Journal of the Acoustical Society of America* **114**(2):1143-1154.
- Møhl, B., M. Wahlberg, P. T. Madsen, L. A. Miller, and A. Surlykke. 2000. Sperm whale clicks: directionality and source level revisited. *Journal of the Acoustical Society of America* **107**(1):638-648.
- Mullins, J., H. Whitehead, and L. S. Weilgart. 1988. Behaviour and vocalizations of two single sperm whales, *Physeter macrocephalus*, off Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences* **45**(10):1736-1743.
- Nishiwaki, M., S. Ohsumi, and Y. Maeda. 1963. Change of form in the sperm whale accompanied with growth. *Scientific Reports of the Whales Research Institute* **17**:1-14.
- Norris, K. S., and G. W. Harvey. 1972. A theory for the function of the spermaceti organ of the sperm whale (*Physeter catodon* L.). *NASA Special Publication* **262**:397-417.
- Nosal, E.-M., and L. N. Frazer. 2006. Track of a sperm whale from delays between direct and surface-reflected clicks. *Applied Acoustics* **67**(11):1187-1201.

- Ohsumi, S. 1966. Sexual segregation of the sperm whale in the North Pacific. Scientific Reports of the Whales Research Institute, Tokyo **20**:1-16.
- Ohsumi, S. 1971. Some investigations on the school structure of sperm whale. Tokyo.
- Oliveira, C., M. Wahlberg, M. Johnson, P. J. O. Miller, and P. T. Madsen. 2013. The function of male sperm whale slow clicks in a high latitude habitat: communication, echolocation, or prey debilitation? Journal of the Acoustical Society of America **133**(5):3135-3144.
- Pitman, R. L., L. T. Ballance, S. I. Mesnick, and S. J. Chivers. 2001. Killer whale predation on sperm whales: observations and implications. Marine Mammal Science **17**(3):494-507.
- Rendell, L., and H. Whitehead. 2001. Culture in whales and dolphins. Behavioral and brain sciences **24**:309-382.
- Rendell, L. E., and H. Whitehead. 2003. Vocal clans in sperm whales (*Physeter macrocephalus*). Proceedings of the Royal Society of London B: Biological Sciences **270**(1512):225-231.
- Rice, D. W. 1989. Sperm whale, *Physeter macrocephalus* (Linnaeus, 1758). Pages 177-233 in S. H. Ridgway and R. Harrison, editors. Handbook of Marine Mammals. Academic Press, London, UK.
- Richard, K. R., M. C. Dillon, H. Whitehead, and J. M. Wright. 1996. Patterns of kinship in groups of free-living sperm whales (*Physeter macrocephalus*) revealed by multiple molecular genetic analyses. Proceedings of the National Academy of Sciences of the United States of America **93**(16):8792-8795.
- Richter, C., S. Dawson, and E. Slooten 2006. Impacts of commercial whale watching on male sperm whales at Kaikoura, New Zealand. Marine Mammal Science **22**(1):46-63.
- Richter, C. F., S. M. Dawson, and E. Slooten 2003. Sperm whale watching off Kaikoura, New Zealand: effects of current activities on surfacing and vocalisation patterns.
- Sagnol, O., C. Richter, F. Reitsma, and L. H. Field. 2015. Estimating sperm whale (*Physeter macrocephalus*) daily abundance from a shore-based survey within the Kaikoura submarine canyon, New Zealand. New Zealand Journal of Marine and Freshwater Research **49**(1):41-50.
- Sagnol, O. J. Y., C. Richter, L. H. Field, and F. Reitsma. 2014. Spatio-temporal distribution of sperm whales (*Physeter macrocephalus*) off Kaikoura, New Zealand, in relation to bathymetric features. New Zealand Journal of Zoology **41**(4):234-247.
- Steiner, L., L. U. Lamoni, M. A. Plata, S. K. Jensen, E. Lettevall, and J. C. D. Gordon. 2012. A link between male sperm whales, *Physeter macrocephalus*, of the Azores and Norway. Journal of the Marine Biological Association of the UK **92**(8):1751-1756.
- Teloni, V., M. P. Johnson, P. J. O. Miller, and P. T. Madsen. 2008. Shallow food for deep divers: dynamic foraging behavior of male sperm whales in a high latitude habitat. Journal of Experimental Marine Biology and Ecology **354**(1):119-131.
- Thomas, J. A., C. F. Moss, and M. Vater. 2004. Echolocation in bats and dolphins. University of Chicago Press.

- Tyack, P. L., and C. W. Clark. 2000. Communication and acoustic behavior of dolphins and whales. Pages 156-224 in W. W. L. Au, A. N. Popper, and R. R. Fay, editors. Hearing by whales and dolphins. Springer, New York.
- Van der Linde, M. 2010. Long-term monitoring of sperm whales in Kaikoura, New Zealand: data-management, abundance, and population dynamics. MSc thesis. University of Otago, Dunedin, New Zealand.
- Watkins, W. A., M. A. Daher, N. A. Dimarzio, A. Samuels, D. Wartzok, K. M. Fristrup, P. W. Howey, and R. R. Maiefski. 2002. Sperm whale dives tracked by radio tag telemetry. *Marine Mammal Science* **18**(1):55-68.
- Watkins, W. A., and W. E. Schevill. 1977. Sperm whale codas. *Journal of the Acoustical Society of America* **62**(6):1485-1490.
- Watwood, S. I., P. J. O. Miller, M. P. Johnson, P. T. Madsen, and P. L. Tyack. 2006. Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *Journal of Animal Ecology* **75**(3):814-825.
- Weilgart, L., and H. Whitehead. 1993. Coda communication by sperm whales (*Physeter macrocephalus*) off the Galápagos Islands. *Canadian Journal of Zoology* **71**(4):744-752.
- Weilgart, L. S., and H. Whitehead. 1988. Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). *Canadian Journal of Zoology* **66**(9):1931-1937.
- Weir, C. R., A. Frantzis, P. Alexiadou, and J. C. Goold. 2007. The burst-pulse nature of 'squeal' sounds emitted by sperm whales (*Physeter macrocephalus*). *Journal of the Marine Biological Association of the UK* **87**(1):39-46.
- Whitehead, H. 1993. The behaviour of mature male sperm whales on the Galápagos Islands breeding grounds. *Canadian Journal of Zoology* **71**(4):689-699.
- Whitehead, H. 1996. Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioral Ecology and Sociobiology* **38**(4):237-244.
- Whitehead, H. 2003. Sperm whales: social evolution in the ocean. University of Chicago Press.
- Whitehead, H., S. Brennan, and D. Grover. 1992. Distribution and behaviour of male sperm whales on the Scotian Shelf, Canada. *Canadian Journal of Zoology* **70**(5):912-918.
- Whitehead, H., A. Coakes, N. Jaquet, and S. Lusseau. 2008. Movements of sperm whales in the tropical Pacific. *Marine Ecology Progress Series* **361**:291-300.
- Whitehead, H., S. Waters, and T. Lyrholm. 1991. Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. *Behavioral Ecology and Sociobiology* **29**(5):385-389.
- Whitehead, H., and L. Weilgart. 1991. Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. *Behaviour* **118**(3-4):275-296.
- Wikipedia. 2013. Sperm whale (*Physeter macrocephalus*) distribution based on records of whalers and surveyors around the world. ([https://en.wikipedia.org/wiki/Sperm_whale#/media/File:Sperm_whale_distribution_\(Pacific_equirectangular\).jpg](https://en.wikipedia.org/wiki/Sperm_whale#/media/File:Sperm_whale_distribution_(Pacific_equirectangular).jpg)). Accessed on 7 October 2016.

Zimmer, W. M. X., P. L. Tyack, M. P. Johnson, and P. T. Madsen. 2005. Three-dimensional beam pattern of regular sperm whale clicks confirms bent-horn hypothesis. *Journal of the Acoustical Society of America* **117**(3):1473-1485.

2. A function analysis of male sperm whale slow clicks on a male-only foraging habitat

Abstract

Sperm whales (*Physeter macrocephalus*) use a variety of ‘click’ sounds for echolocation and communication. Within these, ‘regular clicks’ function as long range directional echolocation during foraging dives, while ‘creak clicks’ are associated with the final approach prior to prey capture. ‘Coda clicks’ have a communication function, being associated with social bonding within female social units. Males segregate from females during puberty and head toward higher latitudes where they maximise foraging time and spend significantly less time socialising. Once apart from their family units males start using ‘slow clicks’, apparently not used by females, both at lower latitude breeding grounds and at higher latitude male-only foraging habitats, such as that found at Kaikoura, New Zealand. The low frequency spectral characteristics, and the apparent inferior directionality of slow clicks, together with the lack of temporal relationship between these clicks and foraging activities on male foraging grounds, led researchers to consider that these clicks are better suited for communication than for echolocation. Towed hydrophone array and photo-identification data from individually-tracked whales were used to gather information on the use of slow clicks in this male-only foraging ground. Slow clicks were analysed as a function of the number of other acoustically-detected whales in the area. Results suggest that having near neighbours results in more vocalisations produced by the focal animals. I also tested slow click function from the echolocation perspective. A correlation between depth and the inter-click interval of a slow click and a regular click at the start of dives indicates a possible echolocation function for slow clicks at the start of dives.

2.1. *Introduction*

Although sperm whales produce a wide variety of sounds, including trumpets, squeals and pips (Goold 1999, Teloni 2005), their vocalisations have been classified into four main click categories. ‘Regular clicks’, also identified as ‘usual clicks’ (Whitehead and Weilgart 1991) or ‘searching clicks’, are used for long range directional echolocation (Møhl et al. 2000, Madsen et al. 2002b). ‘Creak clicks’ (or ‘buzzes’) are associated with short range echolocation prior to prey capture (Gordon 1987, Miller et al. 2004), and are analogous to the buzzes produced by bats while foraging on insects (Griffin et al. 1960). ‘Coda’ clicks, which exhibit regional variation (Weilgart and Whitehead 1997, Antunes et al. 2011), are stereotyped patterns of clicks (Watkins and Schevill 1977) that function for communication and are strongly associated with bonding within female social units, although rarely used by males (Whitehead 2003). The least understood click type is the ‘slow click’, which is only produced by males (Gordon 1987, Mullins et al. 1988, Weilgart and Whitehead 1988, Goold 1999, Madsen et al. 2002b, Barlow and Taylor 2005, Teloni et al. 2008, Oliveira et al. 2013).

Slow clicks were first reported as “clangs” by Gordon (1987) and were later described as “slow clicks” by Weilgart and Whitehead (1988), while Jaquet and colleagues (2001), working with males from Kaikoura in New Zealand, called them “surface clicks” after observing that these clicks were mostly emitted when the whales returned to the surface after foraging dives. Slow clicks have a distinctive metallic sound, long inter-click intervals (ICIs) of several seconds, a lower centroid frequency (roughly between 2–4 kHz) and, like coda clicks, they are longer and less directional than either regular or creak clicks (Madsen et al. 2002b). Slow clicks have been reported in two major behavioural contexts. Gordon (1987) and Weilgart and Whitehead (1988) proposed that slow clicks are used as acoustic display between males when competing for females at breeding grounds, while Mullins et al. (1988) and Madsen et al. (2002b), who made recordings within aggregations of males at higher latitudes (in the absence of females), suggested that they could be used as acoustic display in competition for food, or as courtship practice. Other possible functions for slow clicks have been associated with echolocation (Gordon 1987, Mullins et al. 1988, Goold 1999, Tyack and Clark 2000, Jaquet et al. 2001) and debilitating prey, such as through stunning (Norris and Møhl 1983, Gordon 1987).

Recent research on slow clicks, using data from sound recording d-tags (digital archival tags) placed on males at a male-only foraging ground off Norway (Oliveira et al. 2013), ruled

out the hypothesis that slow clicks serve for prey debilitation due to the lack of temporal a relationship between the

clicks and the whale's foraging phase activities, such as rapid manoeuvring and regular and creak clicks (Miller et al. 2004). Oliveira and colleagues (2013) acknowledge that slow clicks may provide bathymetric information through the characteristic reverberant seafloor echoes that they create, even though their data did not allow them to test this hypothesis. Nevertheless, the context in which slow clicks are produced - mainly during ascent from foraging dives and at the surface - is, according to Madsen and colleagues (2002b) and Oliveira and colleagues (2013), inconsistent with a primary echolocation function for prey and large structures, supporting the idea that slow clicks are primarily a form of long range communication.

In this study I use acoustic and photo-identification data to describe slow click patterns in a male-only foraging ground in the Kaikoura submarine canyon, New Zealand. On the assumption that slow clicks have a probable communication function (Madsen et al. 2002b, Oliveira et al. 2013), I tested the relationship between slow clicks produced by the focal whale, which was acoustically and visually tracked, and the presence of other whales, which were acoustically or visually detected in the area (hereafter 'other whales'). A possible echolocation function was also tested by analysing slow click ICI and its potential for reflecting large structure targets given the whale location - in this case the steep slopes of the Kaikoura canyon (Figure 2.1). The common behaviour of using, what appears to be a single slow click, as the first click of the dive by most of the whales was also investigated with respect to echolocation.

2.2. *Methods*

2.2.1. *Field work*

Field work was done in conjunction with a Department of Conservation (DOC) New Zealand-funded research project, although the questions addressed are independent. The aim of the DOC research was to assess the effects of tourism on the behaviour of sperm whales, in order to decide whether to issue further whale-watching permits in the area (Markowitz et al. 2011).

Acoustical and visual data were collected between October 2009 and June 2011 in the Kaikoura canyon, south of the Kaikoura peninsula, on the East coast of South island of New Zealand. The research area generally overlaps with the local sperm whale boat-based tourism activities, mostly within water depths > 500 m and to c. 12 nm from the coast (Figure 2.1). Field work was completed using a 6 m aluminium boat powered by a 200 hp four-stroke outboard engine, equipped with a raised observation platform which gave a 360° unobstructed view. Whales were located using a directional hydrophone. Once located, they were visually tracked during surfacing, and were tracked by means of a towed hydrophone equipped with acoustic tracking and recording software during foraging dives. The goal of data collection was to get visual and acoustical data from known individuals for as many complete dive cycles as possible. A complete dive cycle was defined as the time between two consecutive fluke-up events (start of dive) from the same animal (Figure 2.2).

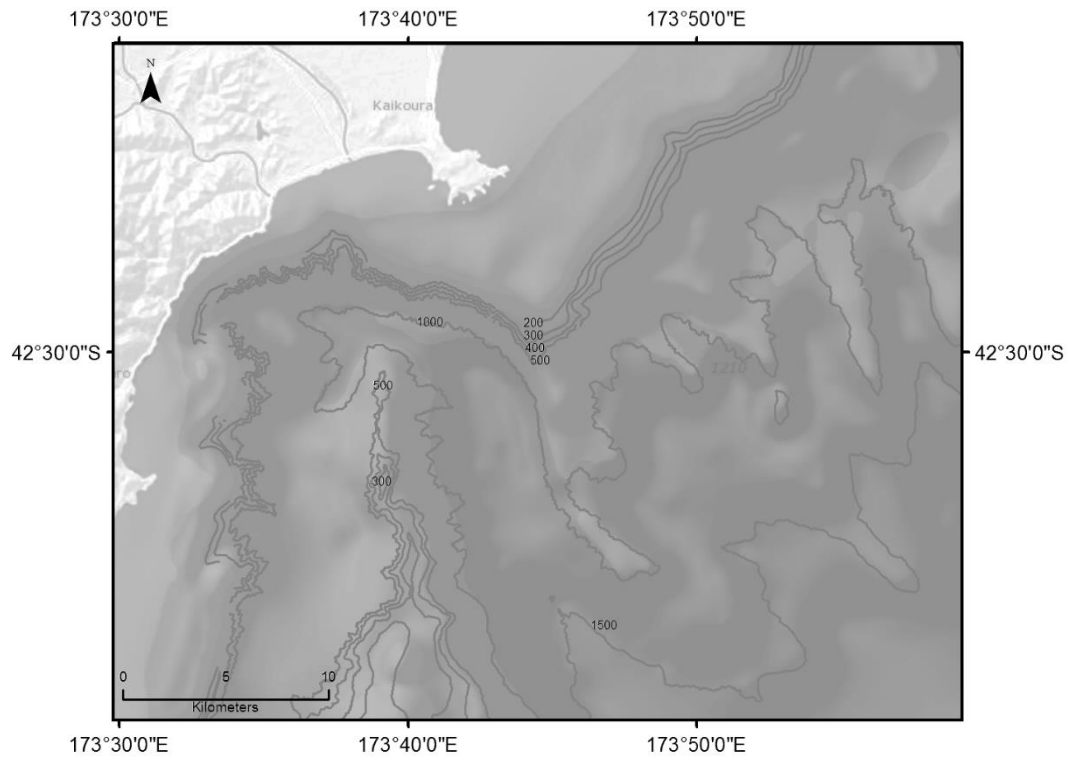


Figure 2.1 – Study area; Kaikoura submarine canyon and associated bathymetry. Bathymetry data courtesy of National Institute of Water and Atmospheric Research (NIWA)

At any given time there are about four foraging adult and sub-adult male sperm whales in the Kaikoura canyon (Sagnol et al. 2014). Here, male sperm whales are thought to share a feeding ground rather than being part of social groups (Lettevall et al. 2002). Interactions, such as synchronised swimming at the surface, are only occasionally observed, which suggests that sperm whales in this region are primarily solitary animals (Lettevall et al. 2002).

While foraging at depth, males' acoustic behaviour is dominated by regular clicks at a rate of about one click per second, and high click rates (creaks) when they encounter a prey target (Jaquet et al. 2001, Miller et al. 2004). Primarily during ascent, but also at the surface, the whales produce bouts of slow clicks (Jaquet et al. 2001) in one of every two dives on average (in this study), and, what appear to be a single slow click as the first click of the dive, in most dives.

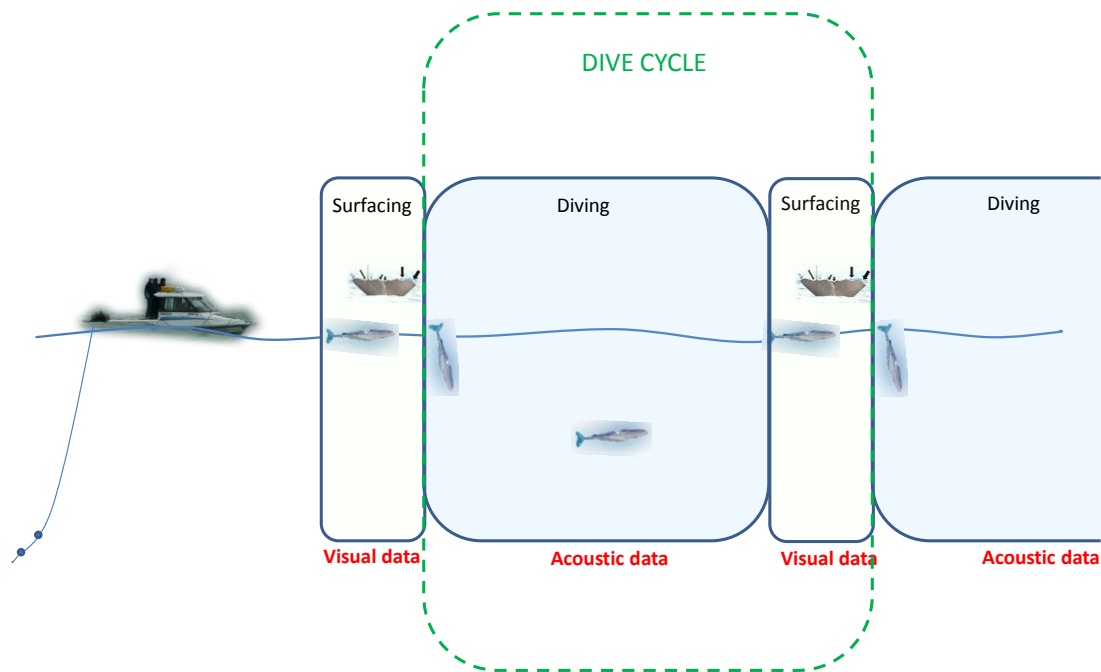


Figure 2.2 – Field data collection scheme; visual data, acoustic data and dive cycle

2.2.2. Acoustic hardware

I used two custom hand-held directional hydrophones (hereafter ‘directional hydrophones’) to locate whales, and to decide on the relative bearing of clicks displayed by the towed hydrophone array software (which shows the bearing, but does not indicate whether the whale is on port or starboard of the boat). Additionally, a towed hydrophone array of two hydrophones was used to make stereo recordings and to acoustically track individual whales while foraging (hereafter ‘hydrophone array’).

The directional hydrophones were composed of a single element located inside a reflective cone covered in polyurethane foam, connected to a high-pass filter and an amplifier in an external box attached to the pole structure. One was built and provided by Dr Steve Dawson from the University of Otago. This was equipped with an AQ-4 hydrophone element with a slightly modified ‘Champ’ amplifier (KC5152: 0.5 Watt headphone amplifier) and ‘PreChamp’ preamplifier (KC5166) providing about 6dB of low-cut filtration at 750 Hz, and 10 dB at 500 Hz. The second directional hydrophone was developed by Ecologic UK and consisted of a High Tech Inc HTI-96-Min hydrophone capsule (Bandwidth 40 Hz to 50 kHz)

mounted on a shock cord within a stainless steel bowl mounted on a pole, with a Magrec HP/24 waterproof monitoring unit as a high pass filter (-3 dB at 1 kHz) and amplification.

The towed hydrophone array was built by Ecologic UK and consisted of a streamlined sensor unit (streamer) towed on a 100 m Kevlar-strengthened cable. The 5 m sensor unit was made of a 35 mm polyurethane tube filled with paraffin oil and contained two Magrec HP-03 spherical hydrophone elements 1 m apart with associated preamplifiers providing 29 dB of gain, each equipped with a low-cut filter set at 100 Hz to reduce low frequency flow noise from the water. The two hydrophones in the array permit the calculation of bearing by using the time of arrival difference from a single click to the different elements (Figure 2.3). The streamer section also contained a Keller 10 bar 4-20 mA pressure sensor to provide information on hydrophone depth.

The analogue acoustic signals from the hydrophone array were amplified on the vessel with a Magrec HP27ST stereo amplifier/filter unit and digitised by a RME Fireface 400 sound card at 96 or 192 kHz. Sample rate was chosen according to the Nyquist–Shannon–Kotelnikov sampling theorem, where sampling rate is at least double the highest frequency of the target signal. This allows the digitisation of the analogue acoustic signal to match the original sperm whale vocalisation frequencies, known to be within the ranges of 0.4 to 20 kHz (Madsen et al. 2002a, Madsen et al. 2002b).

2.2.3. *Photo-identification*

When possible, photos of the tail fluke were taken prior to foraging dives to allow individual identification (Arnbom 1987, Childerhouse et al. 1996), to confirm the animal ID between consecutive surfacings, and to link the surfacing and diving phases from known animals. Photographs were taken using a Canon 40D equipped with a cannon zoom lens EF 100-400mm, f/4.5-5.6 L IS ultrasonic, and a Nikon D300 with an AF-S VR 70-300 mm, f/4.5-5.6 lens. Photos were acquired at a distance of c. 300 m and when the research vessel was directly behind the whale to maximise acquisition of contour information from the edge of the tail fin (fluke). I then manually matched photos to create an identification catalogue. In order to highlight identifiable features for matching purposes, such as skin colour patterns or hidden skin surface irregularities, at times I used image editing, such as zooming and cropping, or brightness and contrast.

2.2.4. *Acoustic data*

To acquire continuous sound recordings while tracking focal whales I used Pamguard software (Gillespie et al. 2009). Pamguard is a passive acoustic monitoring (PAM) software used to detect, localise, track and record marine mammal vocalisations. It displays the real-time bearing of acoustic pulse signals (Figure 2.4), allowing me to track the whale's clicks during its foraging dives while maintaining a close distance to the animal until the subsequent surfacing event. Sound files were set to ten min, stored as a stereo wav-format file, and named with the date and time to the nearest second.

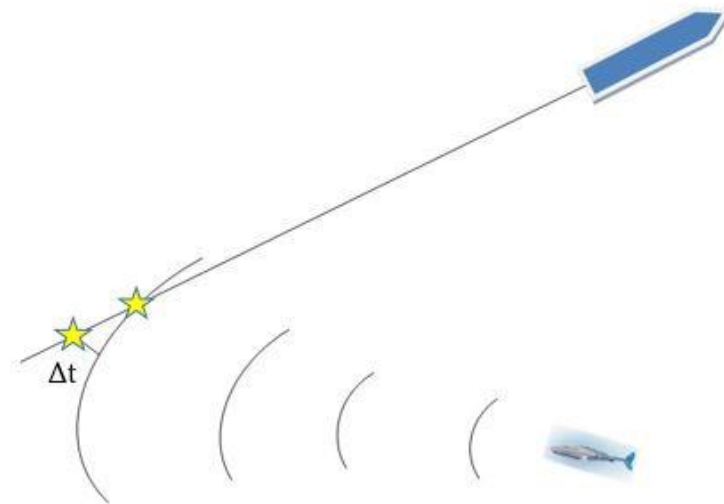


Figure 2.3 – The two elements (stars) of the towed hydrophone array scheme showing the time delay used for calculating the bearing from a detected click (software calculates the bearing but cannot differentiate from which side, port or starboard, it emanates).

2.2.5. *Data extraction*

Acoustical and visual data resulted in about 500 h of sound recordings and about 300 complete dive cycles from 52 individuals. Due to time constraints, the lack of an automated way of auditing the entire dataset with the desired detail and because some sound files were found to be corrupted, a subset of the original database was manually audited for analysis. I audited the acoustic data using Pamguard and Rainbowclick software, the latter of which was specifically developed to analyse sperm whale acoustic data (Gillespie 1997). I extracted regular clicks, creak clicks, slow clicks and coda clicks from the focal whale, and slow clicks and short

sequences of regular clicks from other whales. Regular clicks were defined as clicks with an ICI between 0.1- 2.5 s, except for some slow clicks (see slow click definition below). Creak clicks were defined as clicks with an $ICI \leq 0.1$ s. Slow clicks were distinguished from regular clicks by their $ICI > 2.5$ s, except for clicks that showed a clear centroid frequency between 2–4 kHz (as opposed to about 15 kHz for regular clicks), and were visually confirmed by waveform display as slow clicks (Madsen et al. 2002b). Based on my slow click definition, the lower frequency click often used as the first click of the dive by most whales foraging off Kaikoura was considered to be a slow click. Coda clicks were repeated stereotyped sequences of 2-40 broadband clicks lasting generally < 3 s, adapted from Watkins and Schevill (1977).

Only dives containing sound recordings covering complete dive cycle/s were used for analysis. I used Pamguard to detect clicks within the frequency range of interest (click detector with a ‘Buterworth’ digital high-pass pre-filter at 1500 Hz), while filtering out undesired frequencies, such as low frequency flow and ambient noise, and used a low-pass ‘Buterworth’ at 25 kHz to filter out an unfortunate high frequency electronic interference at about 36 kHz. The resulting ‘click’ files were then used on Rainbowclick for click identification and labelling. Adobe Soundbooth cs5 was used to manually, through visual inspection of spectrogram, find, mark and store, distant slow clicks from other whales otherwise not detected through the filtering process from which ‘click’ files resulted.

I labelled individual clicks during visual and audio inspection of sound files corresponding to complete dive cycles. The information associated with selected clicks included the time, bearing of detection and relative amplitude, which was then stored on a Microsoft Access database. Events were created to label different whales and click types during classification. Where an event by default labels regular clicks, it can hold multiple selectable options that were used to distinguish different click types from the same whale, such as slow clicks, creak clicks or coda clicks.

When it occurs, the first click of the dive, which is produced during or shortly after a fluke-up event (start of dive), shows as a sharp pulse signal ahead of the vessel on the software’s display (Figure 2.4). Since sperm whales are generally silent at the surface, and use regular clicks about every second during foraging dives (Madsen et al. 2002b), one can acoustically distinguish the start of dive of the focal whale by visual confirmation of a new click train starting ahead of the research vessel in the software display. Clicks produced at the surface were defined as those recorded between the surfacing and fluke up times and were determined through code developed in R (Team 2014) that looked for slow clicks during dives, as previously defined, but included 15 s from the previous surfacing time to guarantee the

capture of this first slow click when it occurred at the surface. Slow click ‘events’ were defined as bouts of slow clicks with $ICI \leq 10$ s, or single slow clicks (when $ICI > 10$ s).

Whenever clicks from other whales overlapped in bearing with the focal whale, a combination of the waveform, amplitude and ICI were used to confirm the identification of the focal whale. Although these parameters can change over time within the same individual and during the course of the dive (Møhl et al. 2003, Zimmer et al. 2005), the rate of change is slow and progressive, allowing me to distinguish different individuals. Additionally, I lowered the playback speed of the sound file to distinguish clicks from different whales. If the focal whale and other whale simultaneously went silent for a short period of time (up to 15 s) after a period of overlapped bearings, I continued data extraction if at least two of parameters (waveform, amplitude or ICI), matched the previous clicks from the focal whale, and, using photo-identification data from the following surfacing confirmed the animal’s identity as being the focal whale. Slow clicks and short sequences of regular clicks from other whales were also labelled.

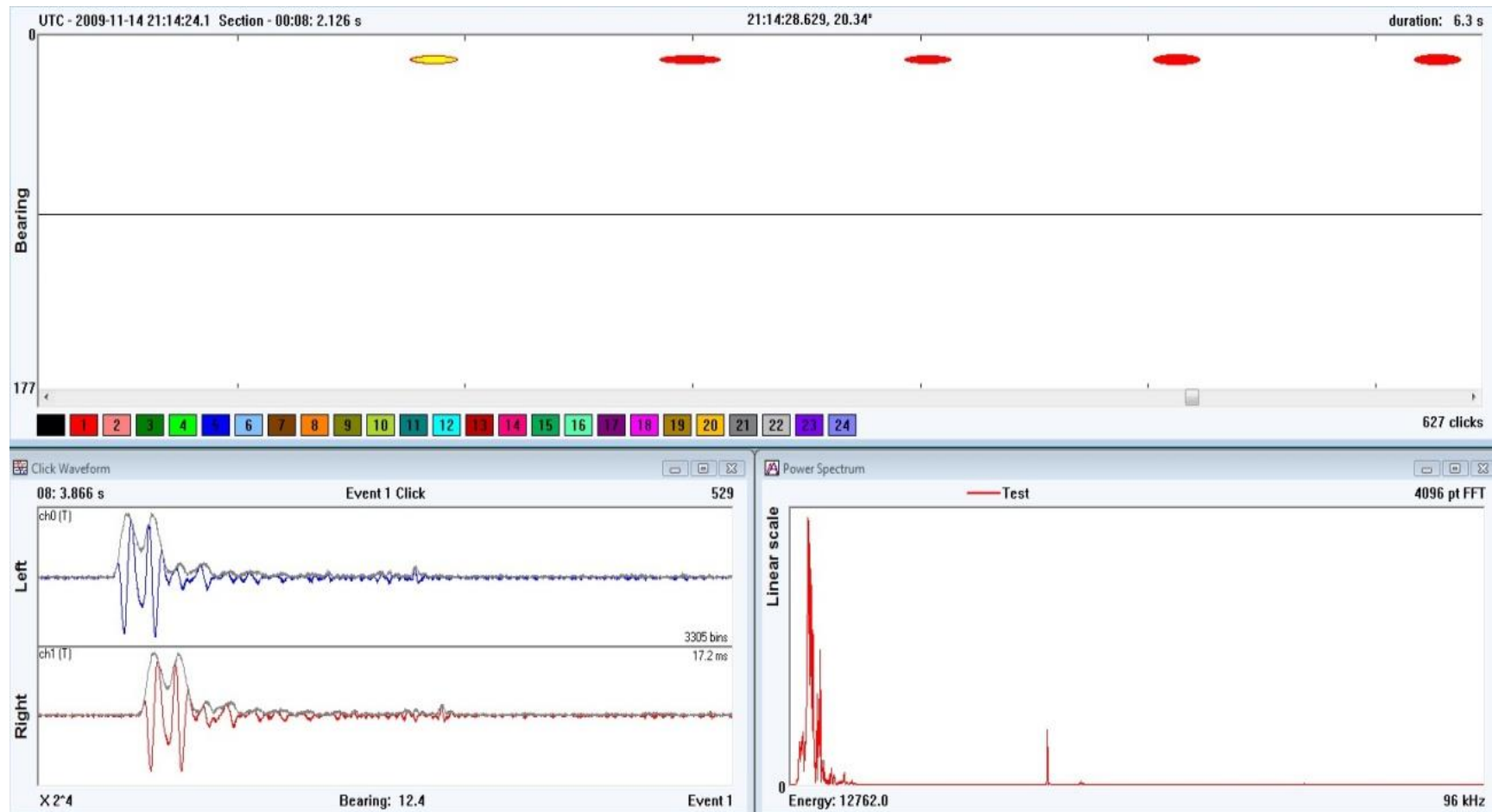


Figure 2.4 – Example of the panel display from the acoustic tracking software Rainbowclick. Top box shows a start of a dive click train; first click of the dive selected in yellow shows ahead of the vessel, bearing zero (top left) corresponds to source directly in front of the vessel. Lower left-hand side box shows the waveform from the selected (yellow) click and the lower right-hand side box shows the power spectrum of the selected click.

2.2.6. *Statistical analyses*

For every 10 min audio file, I estimated the number of other whales present by observing click trains from other whales vocalising simultaneously and at different bearings for at least a few seconds. Within a dive cycle, the estimated number of other whales was used for two separate analyses to determine the effect of the presence of other whales and the production of slow clicks: 1. the maximum number of other whales heard during a dive cycle, and 2. the mean number of other whales heard during a focal animal tracking period (which could include from one to several dive cycles).

The resulting audio characteristics database was coalesced with other data collected in the field, including location, time, and observed behavioural events. Analyses (see Appendix 1 Table 1 for a summary of the variables used for analysis) were completed using lme4 package (Bates et al. 2015) in R 3.1.3 (Team 2014) to run generalised linear mixed models (GLMM). Prior to model-fitting, the distributions of the data were checked. Count data, such as number of slow clicks, slow click events and slow clicks from other whales followed a Poisson distribution. The additional variables of interest were normally distributed.

In order to assess the association between ICIs and depth, as well as between the total number of slow click events emitted by the focal whale (per dive) and the presence of other whales in the area, either the maximum number of slow clicks per dive or the mean number of slow clicks per acoustic follow were analysed using generalised linear mixed models (GLMM). As additional predictors for the number of slow click events produced by the focal whale, I used the number of times the focal whales went silent, the total number of slow clicks from other whales, and depth. As random effects I used intercepts for the focal individual for consecutive dives from the same whale and an independent indexing number (dive number). To compare the number of slow click events produced inside the canyon (scored as 1) with those occurring outside (scored as 0), I used a mixed effects logistic model. Mixed-effects models were chosen to deal with multiple observations on the same individual by fitting these as random effects (Winter 2013).

Model selection for the GLMM assessing the relationship between slow clicks produced by the focal whale and the presence of other whales, was based on comparison of the Akaike information criterion (AIC) between models using different combination of predictors, or by parameter inference using likelihood ratio tests (see modelling details in Appendix 1 Table 1 and 2) when assessing the association between ICIs and depth. The best models were then assessed in terms of how realistic the model predictions were in relation to the whales'

behaviour. Additionally, I used a paired t-test to compare the ICI from slow clicks produced during diving and at the surface, and a one-way analysis of variance (ANOVA) to compare the mean ICI of slow clicks between individuals.

2.3. Results

2.3.1. General patterns

Seventy-eight hours of acoustically tracked whales resulted in 95 complete dives from 14 individual whales (Table 2.1). Total vocalisations from focal whales include 176,875 regular clicks, 741 creaks (feeding attempts), 148 coda clicks, and 586 slow clicks. Based on the mean ICI from slow click events of all animals in all dives, and using the average number of slow clicks per slow click event from all whales in all dives, the whales spent 0.28% of their dive time slow clicking.

The total number of slow clicks from other whales detected on the filtered ‘click’ files was 260 (Table 2.1). However, this number was underestimated because the pre-filtered ‘click’ files did not capture a good part of the distant slow clicks present in the original sound files. For this reason, I used a digital audio editing software, Adobe Soundbooth CS5, to manually, through visual inspection of spectrograms, find, mark and store distant slow clicks from other whales otherwise not detected. During this process, slow clicks were identified as bouts of low frequency clicks (2–4 kHz) displaying regular ICIs between 2.5-10 s, which were accompanied by a strong echo. This resulted on 361 additional slow clicks, more than the number of slow clicks from other whales previously extracted from the filtered ‘click’ files. In order to incorporate the additional slow clicks from other whales in the analysis, and because of technical difficulties in including them into my database with the associated parameters as per prior extractions from ‘click’ files, I used the additional slow clicks detected (361) as a proxy for the number of slow clicks from other whales missed during extractions from the ‘click’ files. Because sperm whales are likely to detect distant slow clicks, during analysis I used different approaches for the independent variable “slow clicks from other whales” (scow) as follow: I ran models using only ‘scow’ detected through the filtered ‘click’ files (as number of scow per dive), and then created three additional scenarios to this variable by adding 25, 50 and 100% more ‘slow clicks from other whales per dive’ as an attempt to make the variable ‘scow’ the most realistic possible. This variable (scow) however, was dropped during modelling selection (see section 2.3.3).

There was a small difference between the total number of slow clicks from the focal whales (586) and the total number of slow clicks from other whales (260+361=621) detected during this study.

One animal was overrepresented in my dataset, with 44 dives out of a total of 95 dives (Table 2.1). This is a known whale which is considered ‘semi-resident’ and was first seen in Kaikoura during summer 1991/92 (Whale NN20 in Childerhouse et al. (1995)), being present and easily accessible more than any other animal.

The presence of regular clicks and creaks, coupled with the regular diving patterns observed (mean surface time of 8.7 min (SD = 2.7) and 40.7 min (SD = 13.5) of diving time), is consistent with foraging behaviour of sperm whales in Kaikoura (Jaquet et al. 2000) and other parts of the world (Gordon 1987). This indicates that foraging was the main activity of the whales during data collection, as expected. A few exceptions where the focal whale spent longer than usual at the surface (up to 23 min) are comparable to the 19 min maximum time at the surface observed by Jaquet and colleagues (2000). However, on rare occasions I observed some whales staying > 1 h at the surface, during which the whales were silent (no clicks heard during these observations) and their respiration rate, which was measured as part of the data collection protocols, generally decreases, suggesting that in these instances the whales were resting. This behaviour was also reported by Teloni and colleagues (2008) at another male-only foraging habitat off Norway.

Two general patterns of slow clicking emerged: (a) the whales started the dive with a single slow click before initiating their regular searching clicks and, (b) the whales emitted slow click bouts toward the end of the dive, presumably on their way to the surface, and occasionally at the surface (Figure 2.5).

On nine occasions, while resting at the surface between foraging dives, the whales emitted slow clicks and regular clicks, sometimes alternating. On one occasion two whales performed at least one complete dive in synchrony (see Chapter 4), surfacing together two times and diving together two times. Prior to surfacing together, at the end of two dives, the whales emitted codas and slow clicks with slow clicks interspersed between some of the codas. This appeared to be a vocal interaction between two males that have been photographed together years apart (the last observation being in 2006, almost four years prior to my observation in 2010, with a possible re-sighting in 2013).

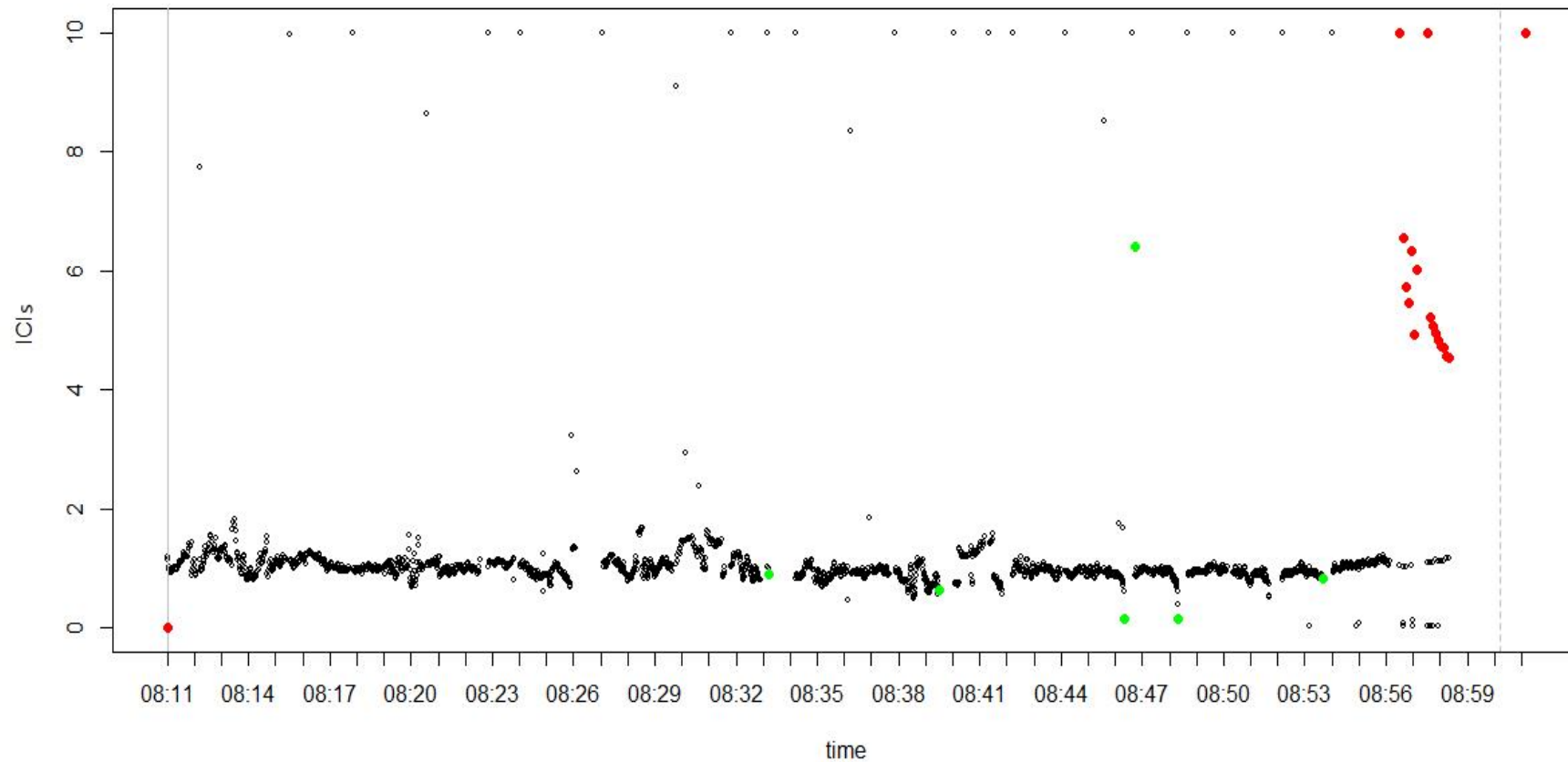


Figure 2.5 – Sperm whale vocalisations from one complete dive cycle, comprising a submerged phase (between vertical lines) and a surfacing phase (to the right of the vertical dotted line). Y axis shows time (s) for the inter-click- interval (ICIs); X axis shows the dive time (min). Black open circles depict regular clicks (searching clicks), green dots are creak events (feeding attempts) and red dots are slow clicks. Note the first click of the dive as a slow click, a bout of slow clicks with longer ICI before surfacing and a single slow click during surfacing.

All whales produced slow clicks, and the focal whales emitted slow clicks in 83 of the 95 (87.4%) analysed dives. In 76.8% of dives, the whales started the dive with a single slow click, as described above (pattern *a*), compared to 24.9% observed by Jaquet and colleagues (2001) in the same study area. Excluding slow clicks that are the first click of the dive, on average the whales used slow clicks (bouts or single clicks) in about 50% of dives. Overall, the whales produced more slow clicks while submerged (74%) compared with surfacing periods (26%) (Table 2.1).

Table 2.1– Summary of counts, percentage or average of slow click (SC) numbers or events per dive from all dives from all individuals, as well as the number of slow clicks from other whales per dive. Totals are given according to the variable. (*) means except for dives starting with a SC.

Whale ID	N dives	N dives starting with a SC (%)	% dives with SC*	N SC (total)	Total N SC events	SC events at surface	SC events diving	SC events / dive	N SC from other whales
1	44	40 (90.9)	47.7	380	87	21	66	1.98	194
2	9	5 (55.6)	11.1	6	6	2	4	0.67	1
3	4	4 (100)	75	34	13	2	11	3.25	0
5	2	2 (100)	50	3	2	0	2	1	0
6	3	2 (66.7)	33.3	8	5	2	3	1.67	0
15	5	3 (60)	40	32	8	1	7	1.6	0
18	2	0	50	2	1	0	1	0.5	9
21	1	1 (100)	100	2	2	0	2	2	0
22	3	3 (100)	0	3	3	2	1	1	0
25	6	3 (50)	66.7	19	9	3	4	1.17	10
26	4	2 (50)	50	13	6	5	1	1.5	20
27	4	4 (100)	100	45	9	0	9	2.25	16
29	5	4 (80)	100	36	13	5	8	2.6	0
36	3	3 (100)	0	3	3	0	3	1	10
Total	95	73 (76.8)	51.7	586	167	43	122	1.585	260

There was no significant difference between the mean ICI from slow clicks produced during diving and at the surface ($t=1.3$, $Df=37.6$, $p=0.186$). The mean ICI for all slow click bouts from all whales in all dives, both submerged and at the surface, was 6.58 s ($SD=1.14$). Whales also showed no significant differences in ICI for slow clicks bouts ($F=0.01$, $Df=26$, $p=0.9$), suggesting that ICIs are not characteristic of specific whales.

2.3.2. *Slow clicks at start of dive*

Sperm whales adjust their initial search range (as indicated by the ICIs of regular clicks) to detect prey layers or the bottom (Fais et al. 2015). My results show that the ICIs from the first ten regular clicks of diving whales were associated with substrate depth at the dive location ($p<0.002$; $Df=5$, see model 1 in Appendix 1 Table 2), in that the mean time between two clicks corresponds approximately to the two-way travel time of the sound to the target of interest (in this case the bottom) and back to the whale. This in line with what other researchers have found in Kaikoura and elsewhere (Jaquet et al. 2001, Madsen et al. 2002b).

Taking into consideration that slow clicks are much less directional than regular clicks (Madsen et al. 2002b), I explored the function of the first slow click of the dive to test the hypothesis that it has an echolocation purpose.

Most sperm whale dives (76.8%) started with a single slow click prior to normal regular click sequences (pattern *a*). I isolated these dives to test if the time (ICI) between the single slow click and the first regular click was also associated with the distance to the bottom at the dive location, as I found to be the case for the first 10 regular clicks of all dives previously tested. The relationship, however, shows a cluster of longer ICIs that appear ‘out of place’ (Figure 2.6) so I tested this using two approaches: 1) using all data (i.e., all ranges of ICIs) and 2) using only ICIs up to 3 s (grouped as 2 in Figure 2.6). When all data were used (approach 1) there was a non-significant weak association between the ICI and depth ($p=0.068$; $Df=5$; model 3, see Appendix 1 Table 2), while using short ICIs (approach 2) showed a strong association between ICI and depth ($p<0.002$; $Df=5$; model 5, see Appendix 1 Table 2), which was similar to the results that used the first 10 regular clicks of each dive (model 1, see Appendix 1 Table 2), suggesting that ICIs between slow clicks and regular clicks at the start of dives may also be used to target the bottom, like regular clicks alone.

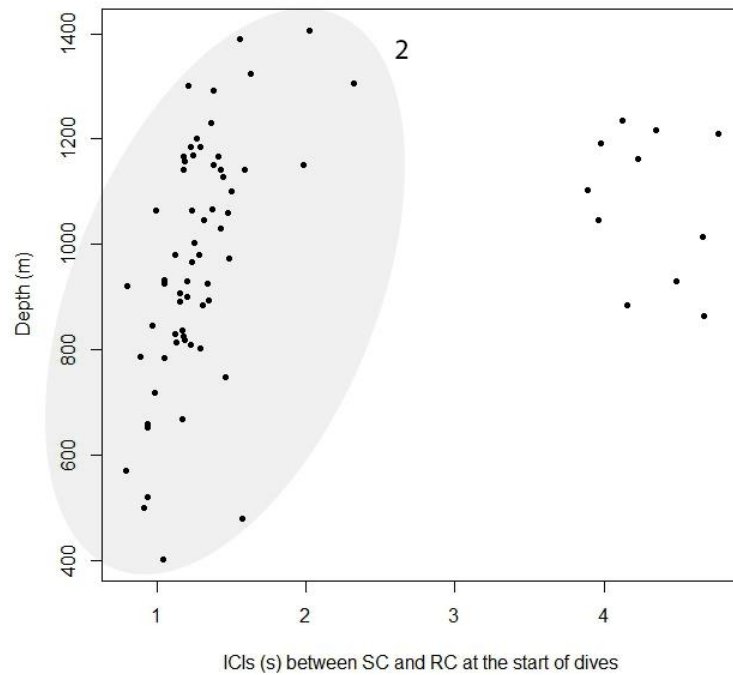


Figure 2.6 – Scatterplot of inter-click interval (ICIs) between a slow click and a regular click at the start of dives, in relation to depth. Selected area (2) indicates subset of data used in approach 2 analysis (see text for details).

To address why at times (about 20%) the ICIs are longer (> 3 s cluster on Figure 2.6), I plotted dive location against a bathymetric map (Figure 2.7) on the premise that, before starting their regular searching clicks, the whales could be waiting for an echo from a reflective feature further afield than the bottom and hence might use long ICIs. I created zones corresponding to the maximum detection range (echolocating distance) driven by the ICI's by using the following equation:

$$(ICI \times c \div 2)$$

where ICI is the inter-click interval, c the assumed constant speed of sound in water (approximately 1500 m^{-1} (Pierce 1981)) and 2 represents the two-way distance travelled by the sound from the whale to the target and back to the whale.

The resulting image (Figure 2.7) is inconclusive about the features on which the whales might be echolocating when using longer ICIs than necessary to detect the seafloor, as it is

evident that they use these when they are in very steep areas, as well as in areas with shallow slopes. That all locations are either on a slope or a valley is expected when foraging in a canyon; however, the scanning distances associated with these ICIs always covered at least an additional slope to that corresponding to the whale's location. The complexity of sound transmission through the water column and the influence of the bathymetry were not taken into consideration during this exercise, and are likely to play a significant role in this simple two-way distance travelled approach.

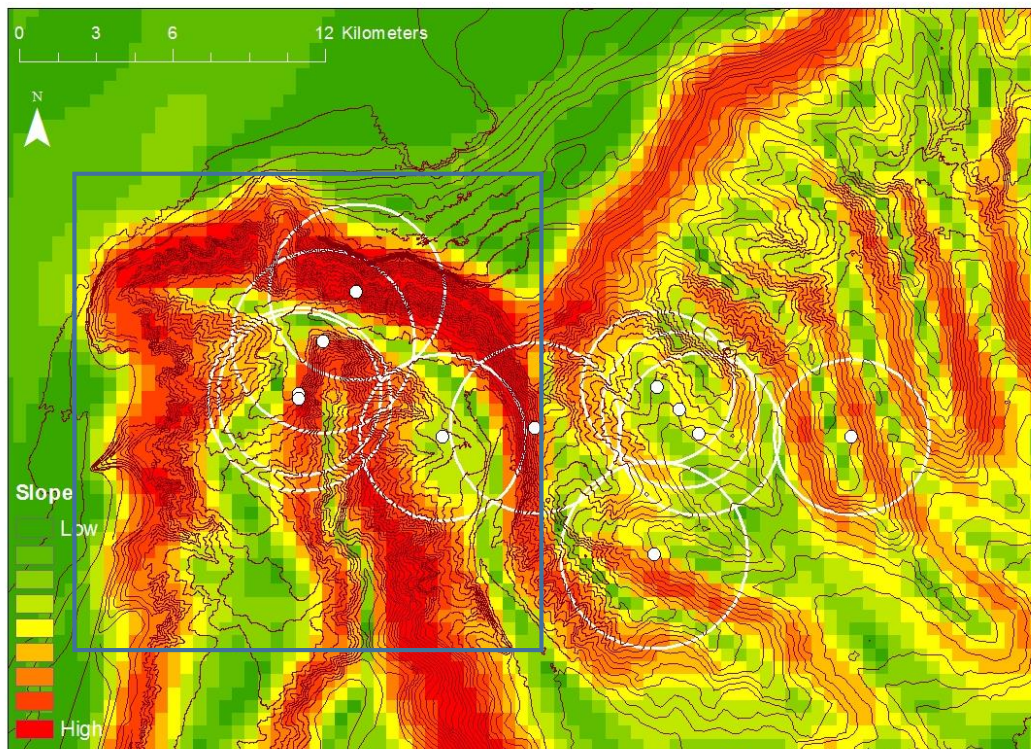


Figure 2.7 – Potential echolocation range (white circles) driven by inter-click intervals between a slow click and a regular click at the beginning of dives of male sperm whales foraging in the Kaikoura canyon. White dots show the dive location of the whales. Blue rectangle defines an enclosed area closer to shore (see text below). Geographic Coordinate System: WGS1984; Projection: Mercator41Swgs.

2.3.3. *Slow click events*

Based on the hypothesis that the function of slow clicks is related to communication, I tested the relationship between the occurrences of slow click events (bouts or single slow clicks) from the focal whale as a function of the presence of other whales in the area. The model that best describes the data (model 7, see Appendix 1 Table 2) predicts an association between the number of slow click events and the mean number of other whales acoustically detected during each follow, where for every extra whale present in the vicinity during the tracking period, the

focal whale produces another 0.2 slow click events per dive ($p = 0.044$; $Df = 88$). This prediction, based on a weak significant positive relationship is, however, difficult to translate into practice, as 0.2 additional slow click events represents a few extra slow clicks from the focal whale for every additional whale in the vicinity. Slow click events were also tested from the echolocation hypothesis perspective, where slow clicks could be used for orientation within the canyon. Here, I compared the number of slow click events produced within the canyon, defined as the enclosed area closer to shore, with those occurring outside the canyon, towards the East (Figure 2.7). No association between whale location and the use of slow clicks was found (model 8: $p = 0.4$; $Df = 91$, see model details in Appendix 1 Table 2).

2.3.4. *Slow click echoes*

One of the most notorious characteristics of slow clicks, besides their sharp metallic sound at times, is the echo (

Figure 2.8). To the human ear the echo from a slow click recorded off Kaikoura sounds robust, is long-lasting (well over a second), and slowly decays.

Although all slow clicks have an associated characteristic echo, at times I could clearly hear the echo but was not able to hear the original slow click, although, when analysing the raw file using a spectrogram it was usually possible to find the original click.

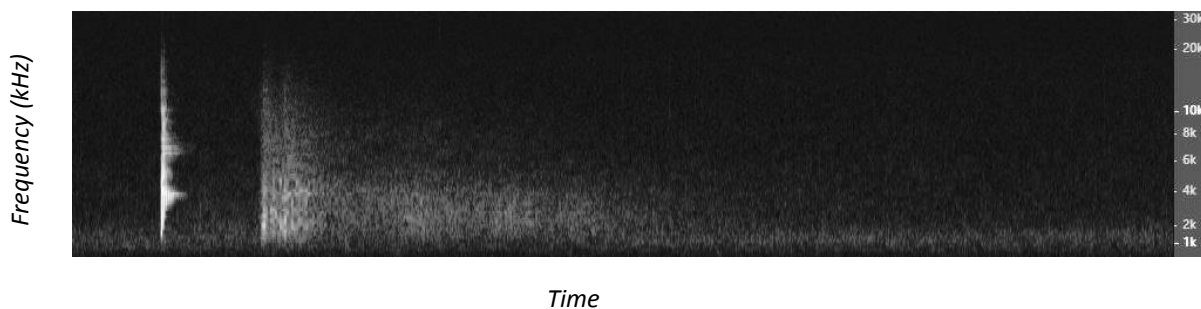


Figure 2.8 – Spectrogram view of a slow click (sharp vertical line) and its echo (lighter decaying shade) lasting about 2 s.

The time delay between a slow click and its echo, presumably from the bottom, was analysed for a sequence of five slow clicks from a single focal whale (Figure 2.9). The gradual increase in the time delay observed suggests that the whale was heading away from the reflective surface causing the echo, at a speed consistent with the vertical movements of sperm

whales (2 m/s; (Teloni 2005)), assuming the first click is the original click and the echo as coming from the seafloor. In this case the whale would have ascended from 1326 m above the seafloor (or other main reflection surface) to 1356 m in about 16 s, travelling at a speed of 1.88 m/s (assuming an underwater speed of sound of 1500 m/s; (Pierce 1981)).

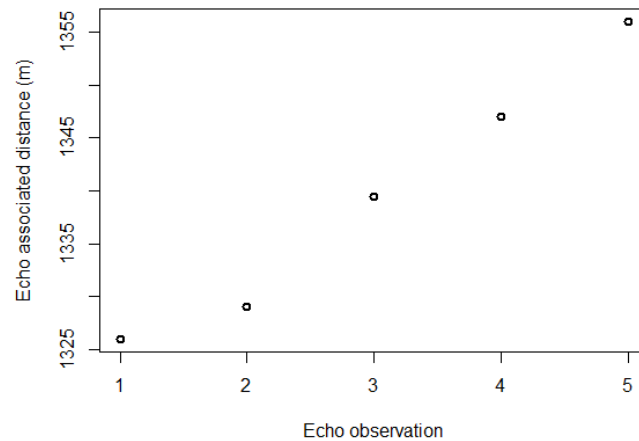


Figure 2.9 – Scatterplot from the analysis of times between slow clicks and its echoes (see text) and the corresponding distances between the whale and the echo reflective surface. For example, the first echo observation suggests the whale is at 1326 m from the reflective sound surface, assumed to be the bottom.

2.4. Discussion

2.4.1. General

The use of slow clicks by foraging sperm whales off Kaikoura seems to fall in two categories: a single slow click is used as the first click of the dive, and/or slow click bouts are emitted in the final phase of dives, presumably when the whales are returning to the surface. I found that all males make use of slow clicks on a daily basis, doing so on almost every dive (87.4%), by using a single slow click at start of dives and/or emitting slow click bouts toward the end of the dive. The majority of slow clicks were produced while the whales were submerged, mostly on their way to the surface, but 26% were during surfacing. Jaquet and colleagues (2001) did not record slow clicks produced at the surface at Kaikoura, and recorded only 24.9% of dives starting with a slow click, compared with the 76.8% that I found. The differences between studies may be due to my close inspection of this particular vocalisation, which may otherwise be confused with a regular click. Alternatively, the first click of the dive, here classified as a slow click, could be a type of click not yet described with characteristics between a regular click (but with a lower frequency and waveform different to regular clicks) and a slow click. Off Nova Scotia, Canada, Mullins and Whitehead (1988) also found slow clicks being produced at the surface. While the whales spent about 0.28% of the time slow clicking in this study, the fact slow clicks were used on a daily basis does not seem to be the rare vocalisation reported by Madsen and colleagues (2002b) working on a Norwegian foraging ground, where males slow clicked in under 1% of 20 h of recordings.

In another study conducted off Norway, Oliveira and colleagues (2013) also report bouts of slow clicks emitted when the whales were ascending to the surface, comparable with my observations and those of Jaquet and colleagues (2001) in Kaikoura. However, Oliveira and colleagues (2013) reported a different slow click pattern at or close to the surface, where clicks were emitted singly or as bouts of up to 3 clicks immediately before or shortly after surfacing. It is tempting to assume that the function of slow clicks emitted very close to the surface in Norway and the single slow click emitted immediately after diving in Kaikoura may have the same function, which may be echolocation and/or communication, in which case this could represent a different and possibly culturally-transmitted way of achieving the same objectives, as found with the use of coda clicks patterns associated with different acoustic clans (Rendell and Whitehead 2003).

2.4.2. *Slow clicks as communication*

Given the consistent use of a slow click as the first click of dives observed in this study, it was often possible to infer a start of a dive from other whales (sometimes visually confirmed) in the vicinity, by observing a start of a new click train from which the first click was a slow click, shown at a different bearing. It seems reasonable to assume that sperm whales would extract this kind of information from their conspecifics. Madsen and colleagues (2002b) estimated that slow clicks may be heard at distances up to 60 km, corresponding to a reach of 11,000 km². If sperm whales can process the information encoded in the time between slow clicks within bouts and their echoes, as well as identify the start of dives from other whales using a slow click as the first click of their dive, they would have access to information about the dive cycle phase of slow clicking animals within their hearing range. Since whales spend most of their time submerged, this may minimise the energy costs associated with synchronising with other whales at the surface (Lettevall et al. 2002), and could be used to coordinate movements (Goold 1999), perhaps for migration purposes. As slow click bouts are emitted at specific depth intervals (Oliveira et al. 2013), the interpretation of echo delays could also encode information about the depth and substrate type within which the vocaliser is foraging, transmitting potential foraging cues.

While communication clicks (codas) have mostly been studied from socialising social units and groups at or close to the surface (see Whitehead (2003) for a review), codas have also been associated with the start and end of foraging dives (Watkins and Schevill 1977, Pavan et al. 2000, Teloni 2005, Frantzis and Alexiadou 2008). After observing that codas were emitted at the end (82.4%) or at the beginning of a dive (17.6%) in 10% of their analysed dives from groups of whales in the Mediterranean, Teloni (2005) suggested that codas may have different functions when produced during foraging compared to codas produced during socialising periods. Frantzis and Alexiadou (2008), that studied codas from males in the Mediterranean, reported similar results to those found by Teloni (2005) regarding the timing patterns of codas produced during foraging, and suggested that codas heard during feeding dive cycles in the Mediterranean, which they termed “dive cycle codas”, may play the same role as slow clicks in male-only feeding grounds. Depending on the context, the author suggests co-ordination, competition, or both, as a function. The slow click time patterns observed in this study are comparable to coda time patterns reported by Teloni (2005) and Frantzis and Alexiadou (2008), and could be used to maintain a foraging area free from other males, as previously suggested (Madsen et al. 2002b, Oliveira et al. 2013). Alternatively, it

may play an important role maintaining cohesion among males within aggregations (Caldwell et al. 1966, Christal and Whitehead 1997), which could be important to co-ordinate migrations when returning to breeding grounds (Rice 1989), while allowing whales to benefit from group behaviour which offers advantages in protection against predators (Elgar 1989) and reduces the risk of an energy shortfall (Beauchamp 2005). The use of slow clicks to maintaining cohesion among males within aggregations is further supported by the lack of defined socializing periods among males (Lettevall et al. 2002), possibly resulting from the different foraging strategies between males and females' social units, where males maximise foraging time (Teloni et al. 2008). Like low frequency communication used by Asian elephants to maintain coordination of groups beyond visual range (Poole et al. 1988), slow clicks in male-only grounds could function in a similar way, preventing animals from staying behind the core of the aggregation.

If slow clicks are used to communicate individual features (Madsen et al. 2002b), and hence potentially used to maintain a foraging area free from other whales, the multi-pulse structure sometimes visible on slow clicks (Lamoni 2012), also observed in the present study, may carry such information in the same way the inter-pulse interval between pulses of regular clicks are used by researchers to estimate the size of the animals by allometric relationship (Gordon 1991, Miller et al. 2013b). Additionally, given slow clicks travel further distances than regular clicks (60 km vs. 16 km; Madsen et al. (2002b)), this would allow reaching animals spread across tens of kilometres within male aggregations (Lettevall et al. 2002).

My results show a positive relationship between number of slow click events, or total number of slow clicks, emitted by the focal whale and the number of whales present in the vicinity. This is consistent with the idea that whales use slow clicks to indicate their presence and location to other whales in order to establish foraging boundaries. However, my observation of two males performing synchronised dives and using codas and slow clicks while in close proximity to each other is inconsistent with whales using slow clicks to establish a foraging area (Chapter 4). This observation suggests that slow clicks used in this context were not intended to keep the other whale away, since the two animals voluntarily maintained a close distance for at least an hour while swimming together, both at the surface and during foraging dives.

The fact that only the echo from some slow clicks could be clearly heard suggests that slow click echoes may be detectable at longer distances than the original slow click. This is important information for calculating the distances travelled by slow clicks. If researchers use

only the sound properties from the original click to model slow click transmission loss, this may not be realistic. Perhaps the first seafloor echo should be added to the ‘equation’.

2.4.3. *Slow clicks as echolocation*

If slow clicks are used for echolocation, their frequency content (around 2 kHz peak frequency; Madsen et al. (2002b)) suggests echolocation of large targets, such as conspecifics or hydrographical and bathymetrical features (Gordon 1987, Mullins et al. 1988, Weilgart and Whitehead 1988, Whitehead 1993, Goold 1999). My observation of the two males foraging together and the increase in number of slow clicks as a function of the number of other whales present in the area suggests that whales may use slow clicks to obtain information on the distance, location and possibly individual features of other whales.

The main argument against echolocation as a function for slow clicks arises from the accepted idea that whales would necessarily use it to find prey during the foraging phase (Oliveira et al. 2013), generally defined as the time between the first and the last creaks (feeding attempts), or as they navigate towards prey patches during descent. The lack of correlation between slow clicks and these foraging phases led Oliveira et al. (2013) to disregard echolocation as a function for slow clicks. Nevertheless, marine mammals are known to adopt movement tactics that maximise the probability of encountering prey (Perrin et al. 2009), and sperm whales are thought to follow a methodical technique when foraging (Laplanche et al. 2005). Since male sperm whale geographic distribution is, more than that of females, associated with slopes (Best 1999, Mizroch and Rice 2013), slow clicks could be a useful tool to keep track of these foraging areas. For example, off Norway, sperm whales appear to use information obtained during previous dives to decide where to invest foraging effort in the next dive (Fais et al. 2015). As slow clicks are performed during ascent, in addition to updating them of their position relative to large structures, this may allow sperm whales to plan the next foraging location, which may also include planning on which direction to travel during surfacing. Slow clicks may reveal the slope orientation or be used to assess drift from currents while ascending, or perhaps help detect ocean fronts that are also associated with sperm whale spatial distribution in Kaikoura (Sagnol 2014).

These data did not allow me to test the echolocation hypothesis in full, although the correlation between depth at the dive location and the ICIs between slow clicks used as the first click of the dive and the following regular click, suggests that sperm whales could be using slow clicks for echolocation. The question of why whales would use a slow click to

target the depth instead of, as previously shown, using regular clicks, is pertinent. That slow clicks are less directional than regular clicks (Madsen et al. 2002b) and show a lasting echo may explain this. Whales could potentially assess broad-scale bathymetrical features from the content of the echo, as the closest adjacent slope relative to their location found on the extended ICIs between the first slow click and regular click on start of dives. This could aid in navigation or update the whale on what it has already identified during slow click bouts produced while ascending. This broad-scale ‘sound visualisation’ may not be possible with the highly directional beam of regular clicks (Møhl et al. 2000). While I found no difference between slow clicks use inside and outside of the canyon, steep slopes within the potential scanning distances suggested by slow clicks ICIs are also present outside the canyon, so the orientation hypothesis can not be fully ruled out. Perhaps comparing slow click patterns use in canyon regions with those used in areas where the bottom is flat and wide could help addressing this hypothesis.

Males from Kaikoura (Miller et al. 2013a) and other parts of the world (Gaskin and Cawthorn 1967, Best 1999) forage on the seafloor at times, but how they decide when to dive to the bottom is unknown. This is an important decision in terms of the trade-off between energy invested and the probability of capturing prey (Doniol-Valcroze et al. 2011). It is possible that the type and duration of echoes from slow clicks encodes information about the seafloor substrate type and helps detect an appropriate location for foraging at the bottom. For example, Chotiros (1997) found that sound pulses penetrating from water into sandy silt become dispersive in the 1-10 kHz band, and acoustic methods using frequencies up to 11 kHz (encompassing slow click frequencies) are used to define and classify sediments during technical surveys (Kim et al. 2004).

The use of slow clicks as an echolocation tool would allow males to track dispersed foraging groups of females helping predicting socialising phases in space and time, which would explain why males slow click for extended periods in breeding grounds (Whitehead 1993), regardless of other information that slow clicks may carry.

Slow click ICIs vary between about 2 - 10 s, depending on study and geographical location (Weilgart and Whitehead 1988, Goold 1999, Jaquet et al. 2001, Madsen et al. 2002b, Barlow and Taylor 2005, Oliveira et al. 2013). The potential scanning distance and the characteristics of their surrounding habitat, assuming echolocation as the function of slow clicks, should be excluded before embarking on other theoretical possible functions. The average of 6.6 s between slow clicks found in this study suggests a scanning distance of about 5 km, which is just over the maximum horizontal distance travelled by sperm whales in one

dive cycle of 3.8 km (Jaquet et al. 2001, Watkins et al. 2002). In this sense the ICI from slow clicks would cover their short-term horizontal movement patterns. For example, when six juvenile male sperm whales were entrapped in shallow and confined waters of Scapa Flow, in the Orkney Islands, they emitted slow clicks with the shortest ICIs so far recorded (2-3 s) (Goold 1999). These could have been attempts to scan the bathymetry within a confined area (hence using shorter ICIs) while several boats shepherded the whales to the open ocean.

It seems that slow clicks have a communication function, in the sense that they announce the presence of a male and its location, possibly detailing the foraging phase of slow clicking animals. However, what other information is encoded by slow clicks, and whether they have different functions in different contexts remains to be explored.

2.5. References

- Antunes, R., T. Schulz, S. Gero, H. Whitehead, J. C. D. Gordon, and L. Rendell. 2011. Individually distinctive acoustic features in sperm whale codas. *Animal Behaviour* **81**(4):723-730.
- Arnbom, T. 1987. Individual identification of sperm whales. Report of the International Whaling Commission **37**: 201-204.
- Barlow, J., and B. L. Taylor. 2005. Estimates of sperm whale abundance in the northeastern temperate Pacific from a combined acoustic and visual survey. *Marine Mammal Science* **21**(3):429-445.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**(1):1-48.
- Beauchamp, G. 2005. Does group foraging promote efficient exploitation of resources? *Oikos* **111**(2):403-407.
- Best, P. B. 1999. Food and feeding of sperm whales *Physeter macrocephalus* off the west coast of South Africa. *South African Journal of Marine Science* **21**(1):393-413.
- Caldwell, D. K., M. C. Caldwell, and D. W. Rice. 1966. Behavior of the sperm whale *Physeter catodon* L. Pages 677-717 in K. S. Norris, editor. *Whales, dolphins and porpoises*. University of California Press, Berkeley.
- Childerhouse, S. J., S. M. Dawson, and E. Slooten. 1995. Abundance and seasonal residence of sperm whales at Kaikoura, New Zealand. *Canadian Journal of Zoology* **73**(4):723-731.
- Childerhouse, S. J., S. M. Dawson, and E. Slooten. 1996. Stability of fluke marks used in individual photoidentification of male sperm whales at Kaikoura, New Zealand. *Marine Mammal Science* **12**(3):447-451.
- Chotiros, N. P. 1997. Dispersion of sound in a sandy silt sediment. *Journal of the Acoustical Society of America* **102**(5):3209-3209.
- Christal, J., and H. Whitehead. 1997. Aggregations of mature male sperm whales on the Galápagos Islands breeding ground. *Marine Mammal Science* **13**(1):59-69.
- Doniol-Valcroze, T., V. Lesage, J. Giard, and R. Michaud. 2011. Optimal foraging theory predicts diving and feeding strategies of the largest marine predator. *Behavioral Ecology* **22**(4):880-888.
- Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews* **64**(1):13-33.
- Fais, A., N. Aguilar de Soto, M. P. Johnson, C. Pérez-González, P. J. O. Miller, and P. T. Madsen. 2015. Sperm whale echolocation behaviour reveals a directed, prior-based search strategy informed by prey distribution. *Behavioral Ecology and Sociobiology* **69**(4):663-674.
- Frantzis, A., and P. Alexiadou. 2008. Male sperm whale (*Physeter macrocephalus*) coda production and coda-type usage depend on the presence of conspecifics and the behavioural context. *Canadian Journal of Zoology* **86**(1):62-75.

- Gaskin, D. E., and M. W. Cawthorn. 1967. Diet and feeding habits of the sperm whale (*Physeter catodon* L.) in the Cook Strait region of New Zealand. *New Zealand Journal of Marine and Freshwater Research* **1**(2):156-179.
- Gillespie, D. 1997. An acoustic survey for sperm whales in the Southern Ocean Sanctuary conducted from the RSV Aurora Borealis. *Reports of the International Whaling Commission* **47**:897-907.
- Gillespie, D., D. K. Mellinger, J. C. D. Gordon, D. McLaren, P. Redmond, R. McHugh, P. W. Trinder, X. Y. Deng, and A. Thode. 2009. PAMGUARD: Semiautomated, open source software for real-time acoustic detection and localisation of cetaceans. *Journal of the Acoustical Society of America* **125**(4):2547.
- Goold, J. C. 1999. Behavioural and acoustic observations of sperm whales in Scapa Flow, Orkney Islands. *Journal of the Marine Biological Association of the UK* **79**(3):541-550.
- Gordon, J. C. D. 1987. Sperm whale groups and social behaviour observed off Sri Lanka. PhD thesis. University of Cambridge, Cambridge, England.
- Gordon, J. C. D. 1991. Evaluation of a method for determining the length of sperm whales (*Physeter catodon*) from their vocalizations. *Journal of Zoology* **224**(2):301-314.
- Griffin, D. R., F. A. Webster, and C. R. Michael. 1960. The echolocation of flying insects by bats. *Animal Behaviour* **8**(3-4):141-154.
- Jaquet, N., S. Dawson, and L. Douglas. 2001. Vocal behaviour of male sperm whales: why do they click? *Journal of the Acoustical Society of America* **109**(5):2254-2259.
- Jaquet, N., S. Dawson, and E. Slooten. 2000. Seasonal distribution and diving behaviour of male sperm whales off Kaikoura: foraging implications. *Canadian Journal of Zoology* **78**(3):407-419.
- Kim, G. Y., M. D. Richardson, D. L. Bibee, D. C. Kim, R. H. Wilkens, S. R. Shin, and S. T. Song. 2004. Sediment types determination using acoustic techniques in the northeastern Gulf of Mexico. *Geosciences Journal* **8**(1):95-103.
- Lamoni, L. U. 2012. "Boy-talk": acoustic characterisation of sperm whale slow clicks in a male-only high latitude feeding ground. MRes thesis. University of St Andrews, St Andrews, Scotland.
- Laplanche, C., O. Adam, M. Lopatka, and J.-F. Motsch. 2005. Male sperm whale acoustic behavior observed from multipaths at a single hydrophone. *Journal of the Acoustical Society of America* **118**(4):2677-2687.
- Lettevall, E., C. Richter, N. Jaquet, E. Slooten, S. Dawson, H. Whitehead, J. Christal, and P. M. Howard. 2002. Social structure and residency in aggregations of male sperm whales. *Canadian Journal of Zoology* **80**(7):1189-1196.
- Madsen, P. T., R. Payne, N. U. Kristiansen, M. Wahlberg, I. Kerr, and B. Møhl. 2002a. Sperm whale sound production studied with ultrasound time/depth-recording tags. *Journal of Experimental Biology* **205**(Pt13):1899-1906.
- Madsen, P. T., M. Wahlberg, and B. Møhl. 2002b. Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and communication. *Behavioral Ecology and Sociobiology* **53**(1):31-41.

- Markowitz, T. M., C. F. Richter, and J. C. D. Gordon. 2011. Effects of tourism on the behaviour of sperm whales inhabiting the Kaikoura Canyon. Report submitted to the New Zealand Department of Conservation by PACE-NZRP, Kaikoura Sperm Whale and Tourism Research Project, 20 December 2011, 121 pp.
- Miller, B. S., S. Dawson, and R. Vennell. 2013a. Underwater behavior of sperm whales off Kaikoura, New Zealand, as revealed by a three-dimensional hydrophone array. *Journal of the Acoustical Society of America* **134**(4):2690-2700.
- Miller, B. S., A. Growcott, E. Slooten, and S. M. Dawson. 2013b. Acoustically derived growth rates of sperm whales (*Physeter macrocephalus*) in Kaikoura, New Zealand. *Journal of the Acoustical Society of America* **134**(3):2438-2445.
- Miller, P. J. O., M. P. Johnson, and P. L. Tyack. 2004. Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. *Proceedings of the Royal Society of London B: Biological Sciences* **271**(1554):2239-2247.
- Mizroch, S. A., and D. W. Rice. 2013. Ocean nomads: distribution and movements of sperm whales in the North Pacific shown by whaling data and discovery marks. *Marine Mammal Science* **29**(2):E136-E165.
- Møhl, B., M. Wahlberg, P. T. Madsen, A. Heerfordt, and A. Lund. 2003. The monopulsed nature of sperm whale clicks. *Journal of the Acoustical Society of America* **114**(2):1143-1154.
- Møhl, B., M. Wahlberg, P. T. Madsen, L. A. Miller, and A. Surlykke. 2000. Sperm whale clicks: directionality and source level revisited. *Journal of the Acoustical Society of America* **107**(1):638-648.
- Mullins, J., H. Whitehead, and L. S. Weilgart. 1988. Behaviour and vocalizations of two single sperm whales, *Physeter macrocephalus*, off Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences* **45**(10):1736-1743.
- Norris, K. S., and B. Møhl. 1983. Can odontocetes debilitate prey with sound? *American Naturalist* **122**(1):85-104.
- Oliveira, C., M. Wahlberg, M. Johnson, P. J. O. Miller, and P. T. Madsen. 2013. The function of male sperm whale slow clicks in a high latitude habitat: communication, echolocation, or prey debilitation? *Journal of the Acoustical Society of America* **133**(5):3135-3144.
- Pavan, G., T. J. Hayward, J. F. Borsani, M. Priano, M. Manghi, C. Fossati, and J. C. D. Gordon. 2000. Time patterns of sperm whale codas recorded in the Mediterranean Sea 1985-1996. *Journal of the Acoustical Society of America* **107**(6):3487-3495.
- Perrin, W. F., B. Würsig, and J. G. M. Thewissen. 2009. *Encyclopedia of marine mammals*. 2nd edition. Academic Press.
- Pierce, A. D. 1981. *Acoustics: an introduction to its physical principles and applications*. McGraw-Hill Book Company, New York.
- Poole, J. H., K. Payne, W. R. Langbauer Jr, and C. J. Moss. 1988. The social contexts of some very low frequency calls of African elephants. *Behavioral Ecology and Sociobiology* **22**(6):385-392.
- Rendell, L. E., and H. Whitehead. 2003. Vocal clans in sperm whales (*Physeter macrocephalus*). *Proceedings of the Royal Society of London B: Biological Sciences* **270**(1512):225-231.

- Rice, D. W. 1989. Sperm whale, *Physeter macrocephalus* (Linnaeus, 1758). Pages 177-233 in S. H. Ridgway and R. Harrison, editors. Handbook of Marine Mammals. Academic Press, London, UK.
- Sagnol, O. J. Y. 2014. Spatial and temporal distribution of sperm whales (*Physeter macrocephalus*) within the Kaikoura submarine canyon in relation to oceanographic variables. PhD thesis. University of Canterbury.
- Sagnol, O. J. Y., C. Richter, L. H. Field, and F. Reitsma. 2014. Spatio-temporal distribution of sperm whales (*Physeter macrocephalus*) off Kaikoura, New Zealand, in relation to bathymetric features. New Zealand Journal of Zoology **41**(4):234-247.
- Team, R. C. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, 2012. ISBN 3-900051-07-0.
- Teloni, V. 2005. Patterns of sound production in diving sperm whales in the northwestern Mediterranean. Marine Mammal Science **21**(3):446-457.
- Teloni, V., M. P. Johnson, P. J. O. Miller, and P. T. Madsen. 2008. Shallow food for deep divers: dynamic foraging behavior of male sperm whales in a high latitude habitat. Journal of Experimental Marine Biology and Ecology **354**(1):119-131.
- Tyack, P. L., and C. W. Clark. 2000. Communication and acoustic behavior of dolphins and whales. Pages 156-224 in W. W. L. Au, A. N. Popper, and R. R. Fay, editors. Hearing by whales and dolphins. Springer, New York.
- Watkins, W. A., M. A. Daher, N. A. Dimarzio, A. Samuels, D. Wartzok, K. M. Fristrup, P. W. Howey, and R. R. Maiefski. 2002. Sperm whale dives tracked by radio tag telemetry. Marine Mammal Science **18**(1):55-68.
- Watkins, W. A., and W. E. Schevill. 1977. Sperm whale codas. Journal of the Acoustical Society of America **62**(6):1485-1490.
- Weilgart, L., and H. Whitehead. 1997. Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. Behavioral Ecology and Sociobiology **40**(5):277-285.
- Weilgart, L. S., and H. Whitehead. 1988. Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). Canadian Journal of Zoology **66**(9):1931-1937.
- Whitehead, H. 1993. The behaviour of mature male sperm whales on the Galápagos Islands breeding grounds. Canadian Journal of Zoology **71**(4):689-699.
- Whitehead, H. 2003. Sperm whales: social evolution in the ocean. University of Chicago Press.
- Whitehead, H., and L. Weilgart. 1991. Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. Behaviour **118**(3-4):275-296.
- Winter, B. 2013. A very basic tutorial for performing linear mixed effects analyses. Unpublished work <http://www.bodowinter.com/tutorial/bw_LME_tutorial.pdf> Accessed on 29 September 2016.
- Zimmer, W. M. X., P. L. Tyack, M. P. Johnson, and P. T. Madsen. 2005. Three-dimensional beam pattern of regular sperm whale clicks confirms bent-horn hypothesis. Journal of the Acoustical Society of America **117**(3):1473-1485.

3. Slow click structure and its relationship to body size and directionality

Abstract

The function of slow clicks has been puzzling researchers since they were first noted in the nineteen eighties. These acoustic signals are only used by male sperm whales (*Physeter macrocephalus*), both at male-only foraging grounds at high latitudes and at lower latitude breeding grounds. Slow clicks consist of low frequency (2-4 kHz) sharp clicks with a strong reverberation, typically displayed in bouts with inter-click intervals of 3-9 seconds. The function of slow clicks has been hypothesised to be a form of communication, either for sexual purposes, for control over foraging areas, or to maintain group cohesion. It has also been suggested that slow clicks are used to echolocate large structures. Off New Zealand and Norway, which are male-only foraging grounds, slow click bouts are mostly used during the final and surfacing phases of foraging dives. The time difference between consecutive pulses of regular and coda clicks, i.e., the inter-pulse interval (IPI), is related to the size of the sound production apparatus so that its measurement provides a method to acoustically estimate the size of individual whales. I used IPIs of regular clicks were used to estimate the body length of nine males and to test whether the centre frequency of slow clicks is associated with the size of the caller. I also investigated the waveform pulse structure of slow clicks, specifically looking at the occurrence of multiple pulses and whether this also correlated with body size. Although the centre frequency of slow clicks differed among individuals, there was no relationship with body size. Additionally, while 70% of all slow clicks analysed contained multiple pulses, IPI measurements showed no clear relationship to body size. Variation in both amplitude and in the waveform shape within bouts of slow clicks suggest a defined directionality that affects these parameters. Slow-clicking whales may be changing their body orientation to maximize effectiveness of slow clicks, possibly rotating on their longitudinal axis. In doing this, whales could broadcast to specific targets, which may be associated with communication, echolocation, or serve different functions in different contexts.

3.1. Introduction

Male vocalizations are often subjected to sexual selection, and can broadcast both the quality and condition of the caller (Doty and Welch 2001, Christie et al. 2004, Fischer et al. 2004, Vannoni and McElligott 2008). Acoustic signals carrying size-related information of males may be vital, since body size is frequently associated with fighting ability, which in turn may provide males, including sperm whales (Mullins et al. 1988, Whitehead 1993, Tyack and Clark 2000), with better access to mates (Bee and Gerhardt 2001, Reby and McComb 2003) and possibly food resources.

The vocal repertoire of sperm whales is dominated by sharp broadband clicks that are used for echolocation and communication (Norris and Harvey 1972, Watkins and Schevill 1977, Møhl et al. 2003). The structure of the acoustic waveform of most sperm whale clicks includes a series of regularly-spaced sound pulses that decrease in amplitude (Backus and Schevill 1966). Norris and Harvey (1972) proposed a model where the acoustic reflections within the head of a sperm whale explained the multi-pulse structure of clicks. This model was later modified by Møhl (2001), who proposed that the sound pulse generated by the *museau de singe*, or phonic lips, is directed backwards into the spermaceti organ and that, after reaching the frontal sac, the sound pulse is reflected into the junk complex before being directed into the water in front of the whale - the so-called ‘bent horn’ model (Figure 1.2, Chapter 1; Møhl 2001). Adding to the complexity of decrypting potential information from vocalizations, Møhl and colleagues (2003) found that on-axis clicks (clicks recorded on the longitudinal axis of the whale) exhibit a mono-pulsed structure, while Zimmer and colleagues (2005a) noted that pulses from clicks recorded off-axis show a time delay which varies in accordance with the off-axis angle.

Taking into account the speed of sound within the spermaceti organ (Flewellen and Morris 1978, Goold et al. 1996), the time between pulses, or the inter-pulse interval (IPI), relates to the length of the spermaceti organ (Norris and Harvey 1972), which, in turn, is related to the total length of the whale (Nishiwaki et al. 1963). Researchers have exploited the multi-pulse structure of vocalizations by using the IPI of regular and coda clicks to accurately estimate body length from vocalizing individuals (Gordon 1991, Rhinelanders and Dawson 2004, Marcoux et al. 2006) and to measure growth rate (Miller et al. 2013). It is not known, however, if whales are able to decrypt IPI from conspecifics and thus whether they can actually acquire individual-level information, such as body size, from multi-pulse vocalizations.

Apart from the highly directional ‘regular’ clicks, used to find prey, and ‘creak’ clicks, used to home in on prey during foraging (Møhl et al. 2000, Madsen et al. 2002b, Miller et al. 2004), sperm whales also use ‘coda’ clicks and ‘slow’ clicks. Coda clicks lack directionality (Møhl et al. 2003) and have a communicatory function within female social units, but are rarely used by males (Whitehead 2003). The least understood click type, slow clicks, are male-only vocalizations and show distinctive temporal patterns (Mullins et al. 1988, Weilgart and Whitehead 1988, Jaquet et al. 2001). Like codas, they exhibit low directionality (Madsen et al. 2002b, Lamoni et al. 2012). Slow clicks have the lowest frequency among all clicks produced by sperm whales, with centre frequencies between 2-4 kHz, as opposed to 15 kHz for regular and creak clicks (Madsen et al. 2002b), or 8 kHz for coda clicks (Madsen et al. 2002a).

Slow clicks have been observed both at high latitude male-only feeding grounds, where the social structure of males remains poorly understood (Lettevall et al. 2002), and at lower latitude breeding grounds where males move between female social units (Gordon 1987, Whitehead 1993). Because of the context in which slow clicks have been observed, their biological function has been attributed to echolocation (Gordon 1987, Mullins et al. 1988, Tyack and Clark 2000, Jaquet et al. 2001) or communication (Gordon 1987, Mullins et al. 1988, Weilgart and Whitehead 1988, Whitehead 1993, Tyack and Clark 2000, Madsen et al. 2002b, Barlow and Taylor 2005, Oliveira et al. 2013). Proposed communication functions include vocal displays in competition for females at low latitudes (Weilgart and Whitehead 1988, Tyack and Clark 2000) or acoustic display in competition for foraging space at higher latitudes (Mullins et al. 1988, Madsen et al. 2002b). Slow clicks may also serve as contact calls to maintain social cohesion (Goold 1999), which may facilitate reunion prior to group migration to female grounds (Rice 1989). Overall, slow clicks exhibit acoustical and temporal characteristics that favour a function in communication over that of echolocation of prey (Oliveira et al. 2013), and, as they are typically associated with the end of foraging dives (Jaquet et al. 2001, Oliveira et al. 2013), competition for food has also been proposed (Mullins et al. 1988, Madsen et al. 2002b), possibly through signalling the size of the vocalizing competitor.

If slow clicks, which mostly occur in bouts with long inter-click intervals (ICI) of several (3-9) seconds, are used for communication, parameters such as the spectrum frequency, amplitude, or their pulse structure, and the temporal pattern of the ICI (as is the case for coda clicks; (Gero et al. 2016) may independently or conjointly encode the message. However, while the multi-pulsed structure of slow clicks may encode body size-related information, multi-pulsed slow clicks have been reported as being produced infrequently (Madsen et al. 2002b),

and consequently their use in communication remains untested. Nevertheless, my observations on the sperm whales in Kaikoura suggest that multi-pulsed slow clicks are, in fact, quite common and here I explore the relationship between whale body size and slow clicks. I investigated the pulse structure of slow clicks in terms of frequency of occurrence of a multi-pulse structure, the general shape of the pulses, and whether the IPI from slow clicks can be used to estimate the body size of vocalizers, as is the case for regular and coda clicks (Gordon 1991, Rhinelanders and Dawson 2004, Marcoux et al. 2006). I used the IPI of regular searching clicks from individually-identified males foraging off Kaikoura to estimate the body length of nine whales (e.g., Antunes et al. 2010, Caruso et al. 2015). Additionally, because the fundamental frequency of calls from terrestrial vertebrates (Pfefferle and Fischer 2006, Vannoni and McElligott 2008, Ellis and Bercovitch 2011) and marine mammals (Tyack and Clark 2000) often relates to the physical characteristics of the caller, to further investigate whether slow clicks may carry information associated with the size of the individuals, I tested the association between the centre frequency of slow clicks with whale size (Madsen et al. 2002b).

3.2. *Methods*

3.2.1. *Field work*

Acoustical and visual data were collected between October 2009 and June 2011 in the Kaikoura canyon, South of the Kaikoura peninsula, on the East coast of the South island of New Zealand. Data collection and filtering, selection of data for analysis, as well as animal identification and technical details of the acoustic hardware and software, were as described in detail in sections 2.2.1-2.2.4, in Chapter 2. The ‘recording range’ was defined as the estimated distance between the research vessel and the surfacing location of the whale shortly after emitting slow clicks (hereafter ‘estimated distance’).

3.2.2. *Estimating body length from regular clicks*

The use of the IPI to estimate the total body length of sperm whales has become common practice (Antunes et al. 2010, Caruso et al. 2015) and has evolved from manually measuring the distance between pulses from selected clicks (Gordon 1991, Rhinelander and Dawson 2004) to semi-automated methods (Teloni et al. 2007, Antunes et al. 2010). Here, recordings were analysed using a fully automated Pamguard (Gillespie et al. 2009) IPI plugin developed by Miller (2010). The IPI plugin uses the IPI estimation method developed by Teloni et al. (2007), which makes use of cepstrum analysis (Bogert et al. 1963) to detect the time delay between repeated patterns in a broadband signal. Miller’s (2010) IPI plugin provides accurate body length estimates using as few as 84 regular clicks per whale (Growcott et al. 2011). Additionally, this method allows the use of recordings in which the whale’s orientation is unknown because, by averaging the cepstrum of a large number of clicks, the aspect-dependent pulses tend to cancel out, while the pulse at the true IPI is reinforced (Growcott et al. 2011). The ensemble average was used as the best estimate of the IPI (Growcott et al. 2011), which is an estimator of the length of the spermaceti organ (Teloni et al. 2007). The relationship relating IPI and total body length used (Equation 1) was that developed by Miller (2010), based on data from Kaikoura males, to provide a better fit for larger sperm whales (> 11 m) compared with older versions of this equation (Gordon 1991).

Equation 1:

$$T = 1.258I + 5.736$$

Where T = total length and I = IPI

Ten min sound files containing good quality regular searching clicks (about 1 click/s) from the target whale, usually during the first 10 min of the dive, were used for analysis. To ensure that the clicks picked up by the software were emitted by the targeted whale, I used files that had previously been labelled and linked to specific individuals (see section 2.2.5, Chapter 2). In addition, since males foraging off Kaikoura generally surface alone (Childerhouse et al. 1995), the target whale, which was visually monitored at short distances while at the surface, always provided the strongest signal during the start of dives. Pamguard settings allowed further filtering of clicks from other whales by adjusting the click-detector amplitude threshold or the ‘angle-veto’ feature was used to filter out clicks from nearby whales that were showing at different bearings as a consequence of the use of a stereo hydrophone array.

3.2.3. *Estimating body length from slow clicks*

Based on the same principle and method as described above, I selected slow clicks which depicted a multi-pulse structure (pulse ID code 2, 3 and 4; Table 3.1) to test the hypothesis that they may broadcast body-size information. I merged selected slow clicks from individual whales (section 2.2.5; Chapter 2) as a single sound file (wav.) per individual, spaced one second apart, prior to running these files using Miller’s (2010) IPI plugin. I then used the resulting IPI ensemble average in Equation 1 to estimate the total body length of individuals and compared these results to those attained by using regular clicks. The number of slow clicks analysed was considerably lower than that of regular clicks because of the rarer occurrence of slow clicks and because slow clicks lacking a multipulse structure were excluded from the analysis.

3.2.4. *Spectral analysis of slow clicks*

Slow clicks from known individuals (section 2.2.5; Chapter 2) were manually analysed using Raven Pro (Charif et al. 2008). However, the lower frequency clicks often used as the first click of foraging dives, which were considered slow clicks in Chapter 2, were excluded here due to

uncertainty regarding whether these single, lower frequency clicks have the same function as the slow click bouts produced at the end of dives.

Except for whale ID2, for which only two slow clicks were available, the number of slow clicks analysed per whale was either all available slow clicks, or a few long slow click bouts, ensuring at least 13 slow clicks per individual. Slow click bouts were defined as sequences of at least two slow clicks with $ICI \leq 10$ s. Additional slow clicks, which were not considered in Chapter 2, were extracted from the raw database to either increase sample size (ID6) or to avoid interrupting a slow click bout (ID29).

The centre frequency, frequency range and relative amplitude (hereafter 'amplitude') were all measured from the same channel, from the raw sound recordings that had been digitized at 96 or 192 kHz (16 bit). The 'start' and 'end' time of selected slow clicks was defined as the extent of the shaded area on the spectrogram (Figure 3.1). From this, the frequency range and the centre frequency, defined as the frequency that divides the selection into two frequency intervals of equal energy, was obtained. The amplitude was based on the same time selection in the waveform view.

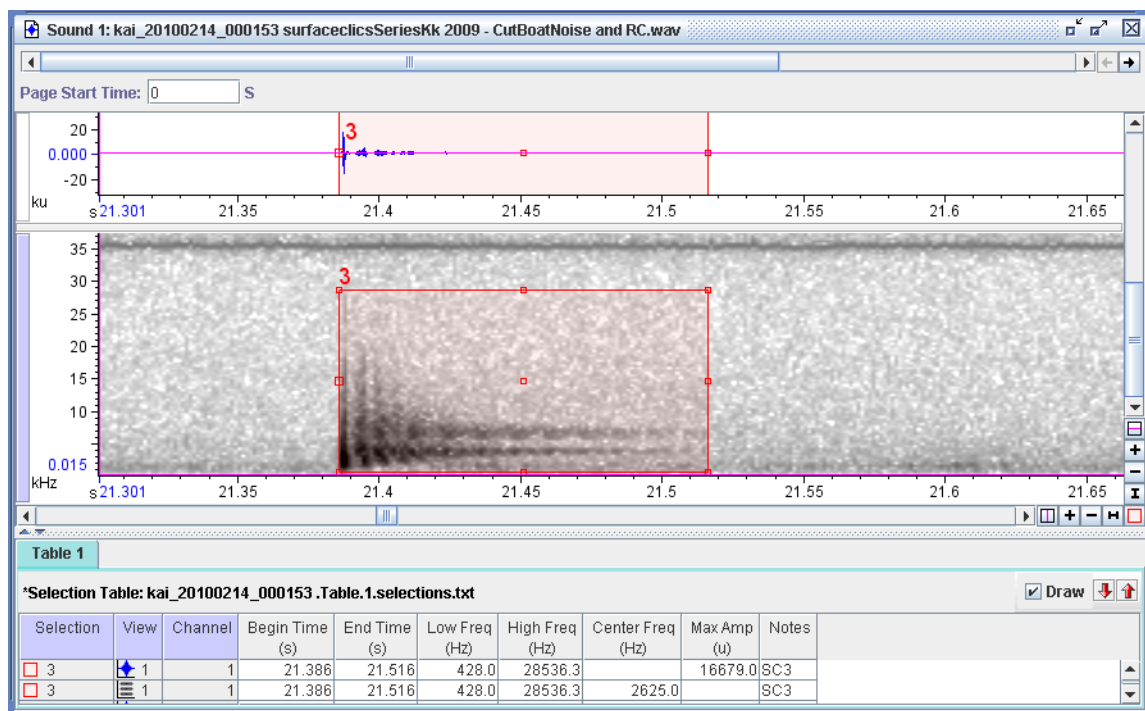
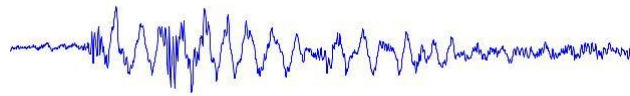
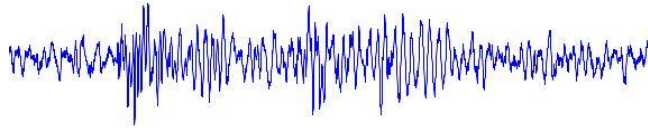

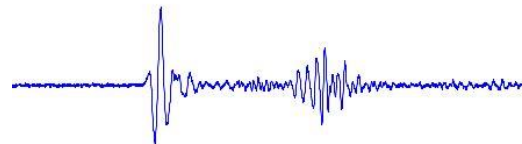
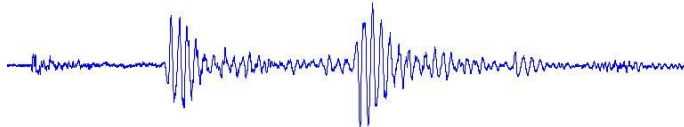


Figure 3.1 – Raven software display showing a section box (red rectangles) highlighting a slow click over time (s). Top panel depicts the click waveform in kilounits (ku), and the lower panel depicts the spectrogram view from the same click in kilohertz (kHz).

3.2.5. *Slow click pulse structure*

To further investigate the pulse structure of slow clicks, I labelled individual clicks according to the occurrence and general shape of their multiple pulses. The assessment of the pulse structure focused on the click waveform, although at times the spectrogram was also used to help identify the occurrence of multiple pulses, as depicted in Figure 3.1. Five categories (Table 3.1) were developed to account for the occurrence and nature of the multi-pulsed structure of slow clicks.

Table 3.1 – Identification key code for the pulse structure of slow clicks and the corresponding waveform pattern. P0 - P3 correspond to the different pulses within sperm whale clicks (Antunes et al. 2010).

Pulse ID code	Description	Waveform pattern
0	No multi-pulse structure clearly distinguishable.	
1	While possible to identify different pulses, there is no clear separation. Generally balanced amplitude between major pulses.	
2	Different pulses are clear, separated and show similar amplitudes.	
3	Different pulses are clear, sharp, with stronger amplitude on the first pulse (P0).	
4	Different pulses are clear, sharp with stronger amplitude on the second pulse (P1) relative to P0.	

3.2.6. *Statistical analyses*

Data normality was assessed using Shapiro-Wilk tests (Shapiro and Wilk 1965). A Pearson correlation test was used to measure the association between the estimated length of the whales and the centre frequency of their slow clicks, and to assess association between total body length estimates using IPIs of regular clicks and those estimates using IPIs of slow clicks. Spearman correlations were used to measure relationships between: 1) the ‘recording range’ and amplitude of slow clicks; 2) the ‘recording range’ and spectral frequency range of slow clicks; 3) the coefficient of variation (CV) of the amplitude of slow clicks per bout and the number of slow clicks per bout; and 4) the CV of the pulse structure of slow clicks (pulse ID code) per bout and the number of slow clicks per bout. The CV of the amplitude and that of the pulse structure within slow click bouts was calculated by dividing the standard deviation by the mean. When comparing the mean estimated recording distance of slow clicks depicting a multi-pulse structure and those that did not show a multi-pulse structure, I used a selection of clicks composed of one slow click from each slow click bout to maximise independence between slow click bouts (samples). The relationship between the CV of the slow click pulse ID code and the number of other whales detected in the area (as calculated in Chapter 2) was analysed using a Kruskal-Wallis test. A Kruskal-Wallis test was also used to compare the centre frequency of slow clicks between different individuals.

3.3. Results

3.3.1. Estimating body length from regular clicks

Based on measurements of IPIs of regular searching clicks, the body lengths of the nine whales measured for this study varied from 13.3 to 15.4 m (Table 3.2), with the mean body length being 14.1 m (SD=0.67).

Table 3.2 – Measured inter-pulse intervals (IPIs) and total body length estimates from regular clicks.

Whale ID	N clicks analysed	IPI peak ensemble average (Min/Max) (ms)	Estimated whale length (SD) (m)
6	873	6.02 (0.06/0.08)	13.31 (0.13)
3	1003	6.21(0.06/0.12)	13.55 (0.17)
29	602	6.25 (0.06/0.04)	13.60 (0.09)
18	1095	6.38 (0.04/0.10)	13.76 (0.13)
27	1253	6.42 (0.08/0.06)	13.81 (0.13)
1	650	6.50 (0.06/0.08)	13.91 (0.13)
25	408	6.92 (0.06/0.08)	14.44 (0.13)
15	661	7.15 (0.04/0.02)	14.73 (0.06)
26	672	7.75 (0.14/0.06)	15.49 (0.19)

3.3.2. Estimating body length from slow clicks

There was no significant correlation ($r=-0.54$, $Df=7$, $p=0.168$) between the estimated body length of individuals based on the IPI of slow clicks and the estimated size based on regular clicks (Figure 3.2).

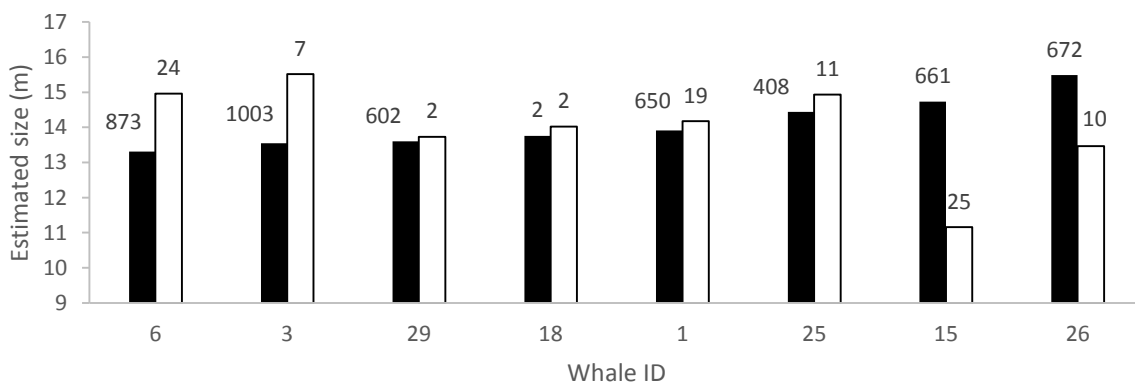


Figure 3.2 – Comparison of total body length estimates of individual sperm whales using regular clicks (black bars) and slow clicks (white bars). Number of clicks used in analysis depicted above each bar.

3.3.3. *Spectral analysis of slow clicks*

The slow clicks originated from 30 bouts with an average of 5.8 (SD=2.5) clicks per bout and a mean ICI of 6 s (SD=1.3). Slow clicks exhibited a mean centre frequency of 3.2 kHz, a mean frequency range of 23.3 kHz (Table 3.3), and the highest frequency reached 64 kHz (range: 0-64).

There was a significant difference in the centre frequency of slow clicks from different individuals ($H=0.779$, $Df=8$, $p<0.002$, $N=9$), although this difference was not related to whale size ($r=0.06$, $Df=1$, $p=0.881$; Figure 3.3).

Table 3.3 – Mean and standard deviation (SD) of the centre frequency (CF) and spectral frequency range (kHz) of slow clicks (SC) from individual male sperm whales.

Whale ID	N SC analysed	Mean CF (SD)	Mean spectral frequency range (SD)
1	21	4.3 (1.8)	22.1 (8.5)
3	17	2.8 (0.4)	32.9 (4.6)
6	25	3.6 (1.1)	40.9 (11.5)
15	32	2.9 (0.6)	22.5 (8.8)
18	2	2.4 (0.3)	32.1 (3.7)
25	15	2.9 (0.4)	21.3 (12.2)
26	13	3.5 (0.5)	13 (5.2)
27	21	2.3 (0.4)	29.3 (8.1)
29	40	3.5 (0.6)	10.2 (6.7)
Total	186	-	-
Total mean	-	3.2 (1)	23.3 (13)

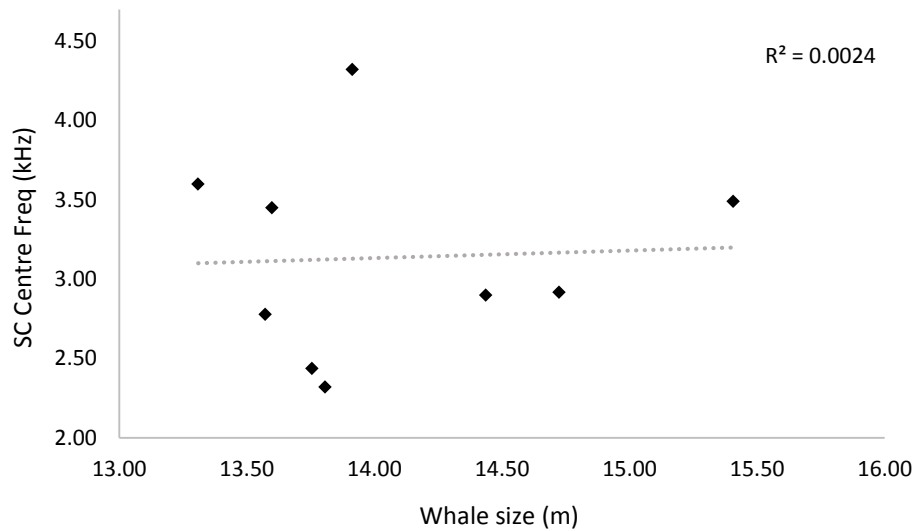


Figure 3.3 – Relationship between the centre frequency of slow clicks of known whales and their estimated body length.

With increasing estimated recording range, there was a significant decrease in the mean spectral frequency range of slow click bouts ($r=-0.70$, $Df=23$, $p<0.0001$; Figure 3.4), and a non-significant negative trend of the mean amplitude per slow click bout ($r=-0.37$, $Df=23$, $p=0.067$; Figure 3.5). The latter relationship is somewhat at odds with underwater frequency-dependent propagation loss, which, for the distances and spectral frequencies involved (up to 1600 m and 2-4 kHz, respectively), should decrease linearly with increasing distance (Figure 3.6).

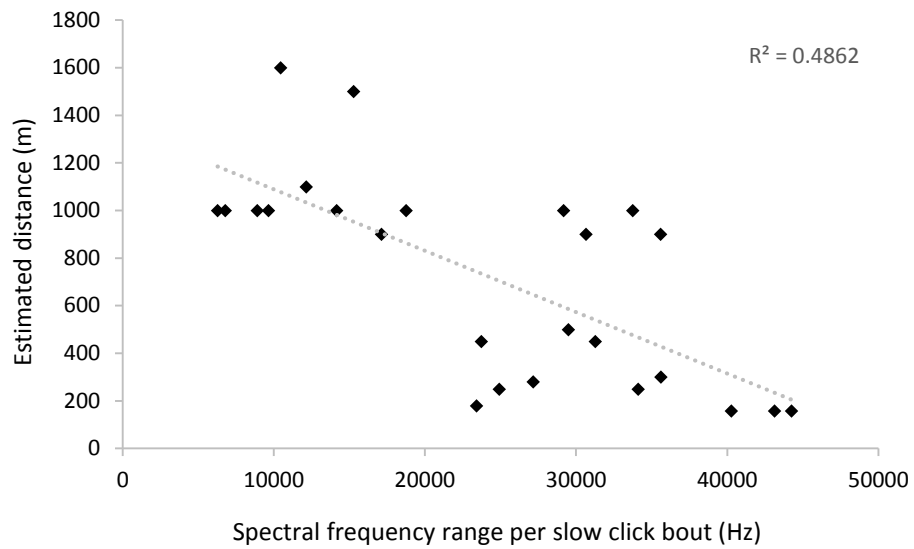


Figure 3.4 – Relationship between the estimated recording distance and the spectral frequency range per slow click bout.

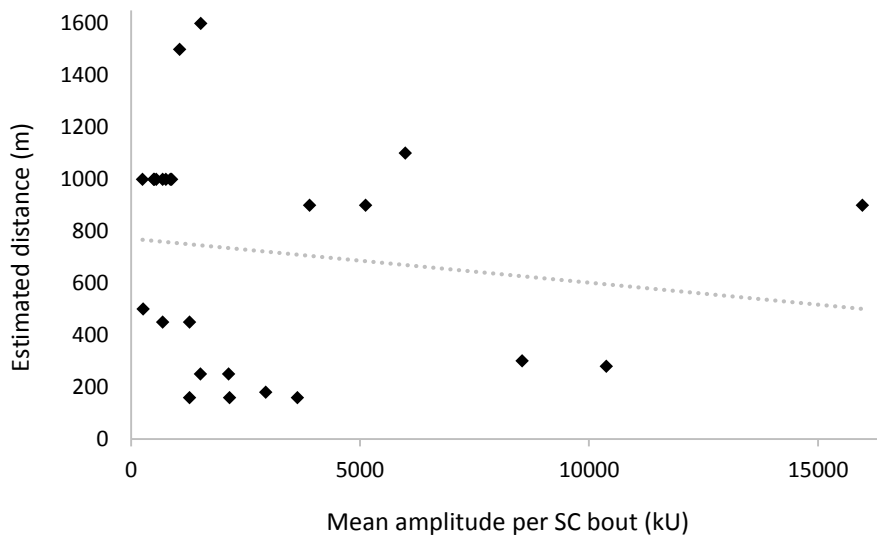


Figure 3.5 – Relationship between the estimated recording distance and the mean amplitude per slow click bout.

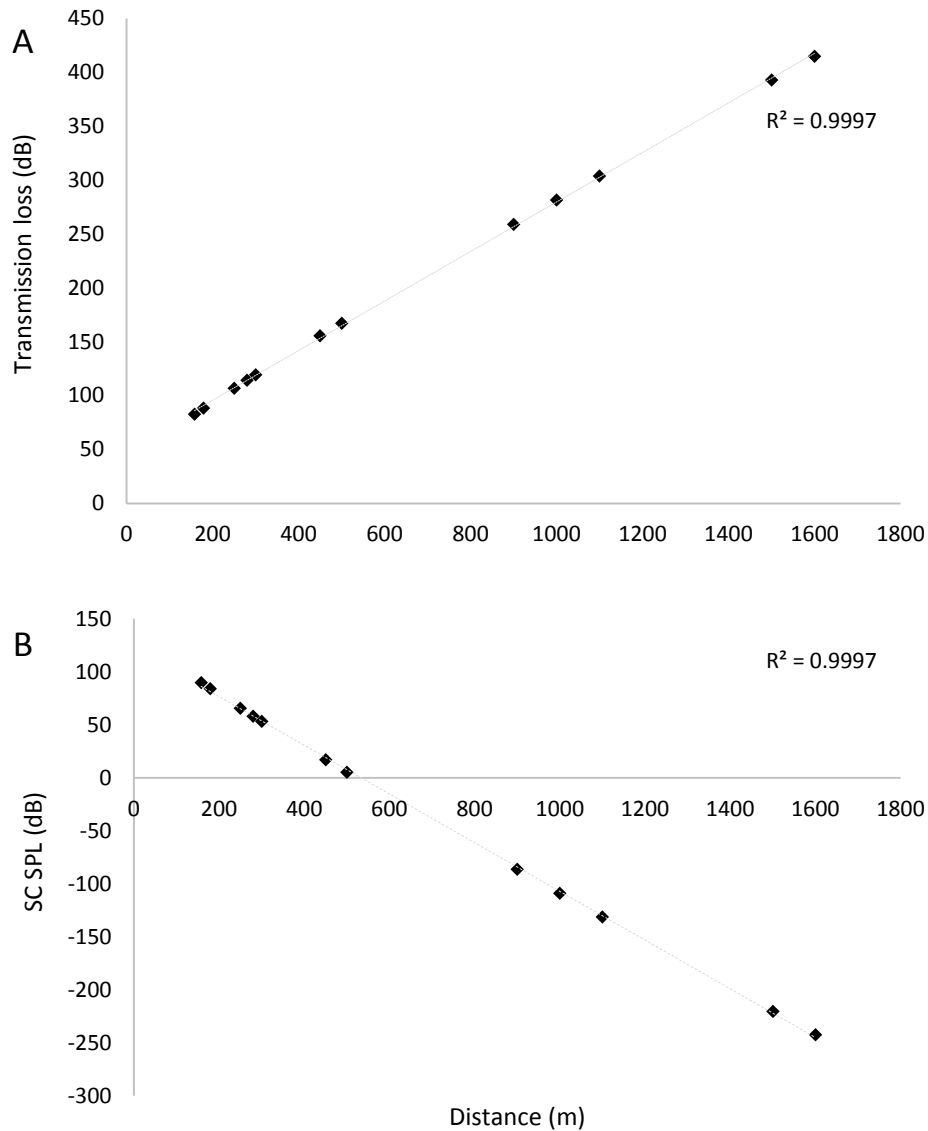


Figure 3.6 – Estimation of geometric spreading, frequency dependent, transmission loss (TL) ($TL = 20\log(R) + \alpha R$; R = range, α = absorption) used in most biosonar systems (Jensen et al. 2009) and applied to the estimated recording distances of the current study. A) Theoretical relationship between transmission loss and distance. Absorption calculations derived from Ainslie and McCollm (1998) algorithms, which required values for Kaikoura temperature, salinity (Bradford 1970) and pH (Jacobson 2005) at the average depth of slow clicking whales (c.a. 150 m (Oliveira et al. 2013)). B) Simulation of the transmission loss of slow clicks (SC) using sound pressure levels (SPL) of 172.4 dB re 1 μ Pa (-3dB endpoint), recorded on tagged males off Norway (Lamoni et al. 2012).

While in 62% of the 26 slow click bouts analysed there was a decrease in amplitude as the whales approached the surface (Figure 3.7A), the amplitude tended to increase in 38% of slow click bouts (Figure 3.7B). The CV of the mean amplitude per slow click bout was 44% (SD=31), illustrating a large variation in amplitude within slow click bouts. However, the CV of amplitude per slow click bout was significantly positively associated with the number of

slow clicks per slow click bout ($r=0.6$, $Df=26$, $p=0.001$), where the greater number of slow clicks produced within a bout, the larger the CV of the amplitude (Figure 3.8B).

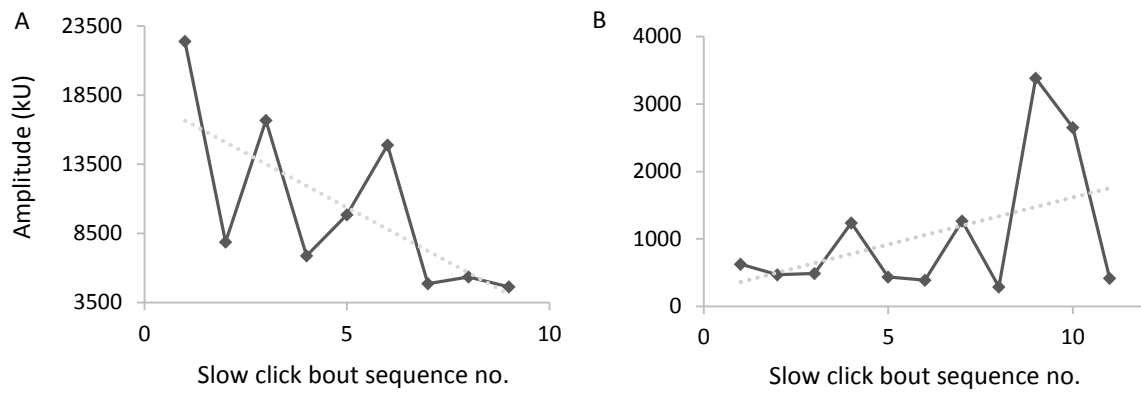


Figure 3.7 – Representative examples of the variation of the amplitude within two slow click bouts. (A) decreasing amplitude, corresponding to 62% of slow click bouts, and (B) increasing amplitude, corresponding to 38 % of bouts.

3.3.4. *Slow click pulse structure*

A multi-pulsed structure was present in 129 of 186 (70%) slow clicks analysed. The most common waveform was that corresponding to code 2, with a clear multi-pulsed structure, followed by code 0, where no clear multi-pulse was observed (Table 3.1 and Table 3.4).

Table 3.4 – Number of slow clicks per pulse structure ID code and the corresponding average estimated recording distances and standard deviation (SD) with respect to the surfacing animal (m).

Pulse ID code	N slow clicks	Average est. distance (SD)
0	57	738 (401)
1	28	943 (425)
2	64	688 (470)
3	26	833 (448)
4	11	370 (382)

There was no difference ($t=-0.4059$, $Df=9.86$, $p=0.693$) between the mean estimated recording distance of slow clicks without multiple pulses (pulse code 0) and those with a multi-pulse structure (codes 1, 2, 3 and 4), suggesting that recording distance did not have an effect on the occurrence of multiple pulses. The mean CV of the pulse structure (i.e., the CV of the number of different pulse ID codes performed by each male in each bout) within slow click bouts was 14% ($SD=18.8$). While some bouts exhibited the same pulse ID in every click (e.g. $CV = 0$; Figure 3.8A), others varied considerably. The CV of the pulse structure per slow click bout tended to be somewhat positively associated with the number of slow clicks per bout ($r=0.33$, $Df=24$, $p=0.102$) (Figure 3.8A). Additionally, there was no association between the way the pulse structure of slow clicks varied (CV) and the number of other whales detected in the area ($H=2.4$, $Df=4$, $p=0.661$, $N=9$).

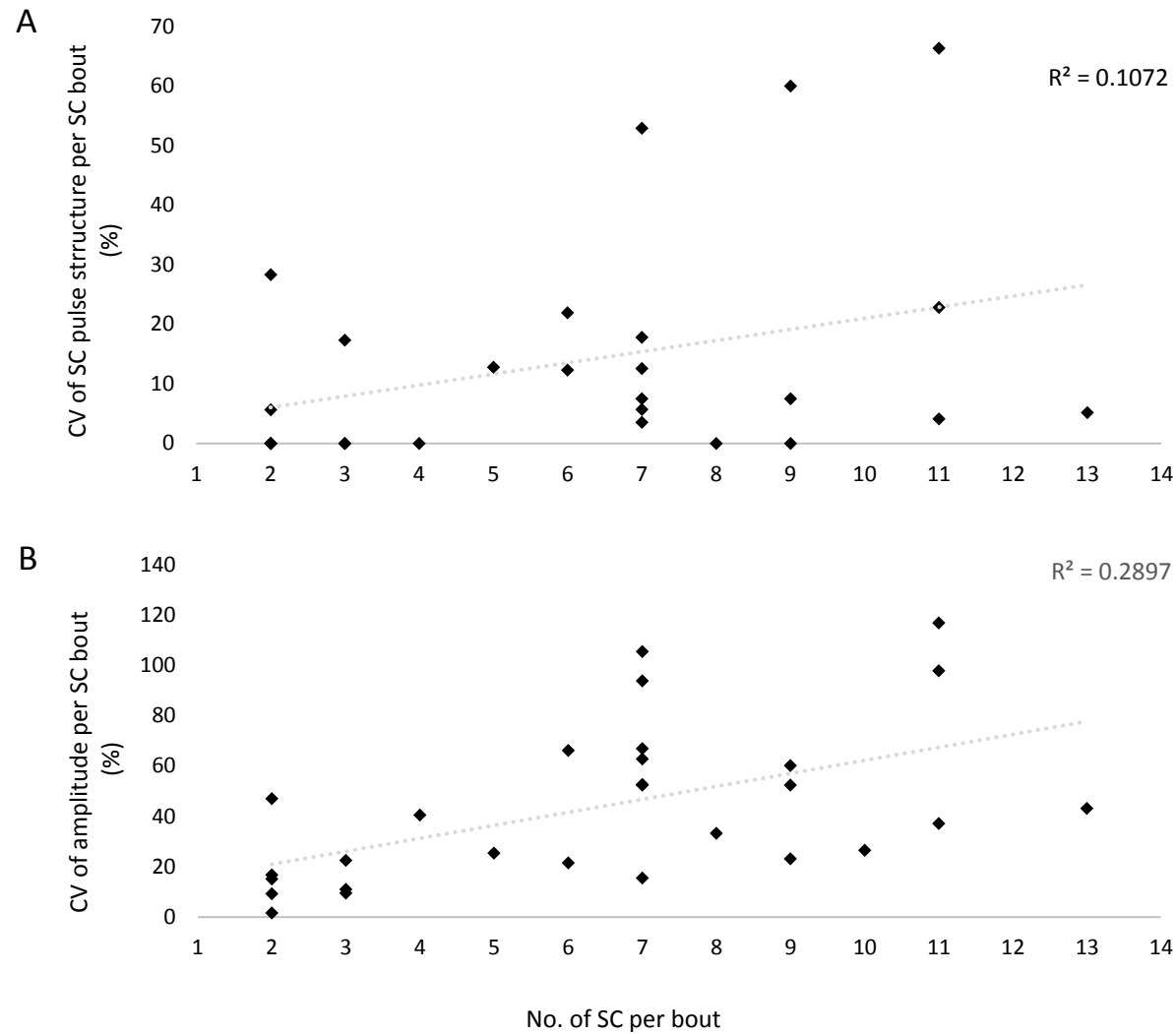


Figure 3.8 – Coefficient of variation (CV) of (A) slow click (SC) pulse structure (as indicated by the pulse ID code -see Table 3.1) per slow click bout as a function of the number of slow clicks per bout and (B) Amplitude per slow click bout as a function of the number of slow clicks per bout.

3.4. Discussion

Data collected during the whaling period shows strong evidence that after dispersal (Mendes et al. 2007, Pinela et al. 2009) males associate in all-male 'schools' of restricted size ranges (Clarke 1956, Gaskin 1970, Ohsumi 1971, Best 1979). Consequently, if the use of slow clicks in male-only grounds serves to maintain group cohesion between individuals (Goold 1999, Madsen et al. 2002b, Oliveira et al. 2013), this may favour these acoustic signals broadcasting body size-related variables. However, the hypothesis that the centre frequency of slow clicks may broadcast body size information (Madsen et al. 2002b, Lamoni et al. 2012) is not supported by my data. I found no relationship between the centre frequency of slow clicks and estimated body length. The centre frequency of slow clicks had not been measured in this region, and its mean (3.2 kHz) is comparable to those found from males off Norway, at around 3 (Madsen et al. 2002b) to 3.5 kHz (Lamoni et al. 2012), suggesting that this characteristic has relatively little geographic variation. If the previous size estimates (Lettevall (1993), cited in Lettevall et al. (2002) for the Norwegian males are still applicable, the larger males from Norway (compared with those in Kaikoura) with similar centre frequencies seem to also support the idea of a lack of correlation between centre frequency and the size of the animals. Nevertheless, the average centre frequency of slow clicks was different among individuals, highlighting the possibility that males could use this information to help in individual recognition (Beecher 1989).

The occurrence of a multi-pulsed structure in 70% of clicks analysed suggests that this is an inherent component of slow clicks, at least in Kaikoura. Madsen and colleagues (2002b) observed a multi-pulsed structure in some of the less reverberant slow clicks, and compared their inter-pulse intervals (IPIs) to those of regular clicks. That the IPI structure of regular clicks is explained by anatomical features of the sound generator (Norris and Harvey 1972, Møhl 2001, Møhl et al. 2003) from which it is possible to accurately estimate total body size of individuals. Gordon (1991) and Growcott et al. (2011) suggest that the IPI of slow clicks may encrypt similar information. However, my attempt to estimate body size using the IPI of slow clicks did not match estimates attained from IPIs of regular clicks from the same individuals. This may be due to a relatively small sample size, since body-length estimates using IPIs from regular clicks require a large number of clicks (Teloni et al. 2007, Miller 2010) to account for changes in the apparent pulse structure of clicks, which vary with the orientation of the whale in relation to the hydrophone (Zimmer et al. 2005a). The difficulty of recording large numbers of slow clicks from the same animal is due to the scarcity with which these occur compared to

regular clicks (Madsen et al. 2002b). In Chapter 2, I found that the number of slow clicks per dive was on average 5.4 clicks/dive ($N_{(\text{dives})}=95$), compared with 1,200 to 2,000 regular clicks (Madsen et al. 2002a, Wahlberg 2002). Because slow-clicking whales are swimming towards the surface (Jaquet et al. 2001, Oliveira et al. 2013), and the boat will rarely, if ever, be located directly above of the whale, all slow clicks are likely recorded from an angle which is off the longitudinal axis up to ninety degrees abeam of the whale (Figure 3.9). This may have biased or restricted the IPI measurements by not covering enough variability to get the correct average of the IPI estimate (Teloni et al. 2007) as perceived by the hydrophone closer to the surface. Additionally, it is possible that only slow clicks perceived from restricted directions broadcast honest advertising (Fitch and Hauser 2003), comparable to those IPIs measured from on-axis regular clicks, which contain IPIs that accurately reflect the size of the whale's head (Møhl et al. 2003, Antunes et al. 2010). Alternatively, since it is unclear how slow clicks are generated (Huggenberger et al. 2016), the resulting IPIs may be derived from a different sound path within the sound generator complex compared to that of regular and coda clicks (Madsen et al. 2002a). In vertebrates, the larger the vocal track length, the lower the fundamental frequency (Lieberman 1984, Fitch 1997). By keeping the phonic lips open after emitting a slow click, sperm whales could extend the total area/volume involved in the click reverberation, from the distal air sac through to the right nasal passage (Figure 1.2; Chapter 1), which could explain the characteristic lower frequency of slow clicks and would imply a different sound path affecting the waveform.

Analysis of the frequency range of slow clicks shows a high frequency component reaching at least 64 kHz. The observed decrease in spectral frequency range with increasing estimated recording distance is explained by sound transmission loss in water, where high frequencies attenuate faster when compared with lower frequencies (Lurton 2002). The frequency range is thus an indicator of distance, and could be used by whales to estimate the proximity of slow-clicking conspecifics. This information, taken together with the amplitude of the slow clicks, may convey information about the sender's location (Morton 1986). The idea that the frequency range might be used as an indicator of distance is supported by the spectrogram display of distant slow clicks (personal observation) identified in section 2.3.1 in Chapter 2. These distant slow clicks showed as dots at low frequencies (*ca.* 2 - 3 kHz) instead of the characteristic vertical bars associated with sperm whale clicks (Whitehead 2003).

The high CV in amplitude found within slow click bouts, as well as the weak negative association between amplitude and estimated recording distance observed, may suggest that slow clicks display enough directionality so that a change in body posture (or recording

location) of slow-clicking whales will affect the expected amplitude decrease with increasing distance, assuming a constant source amplitude reported for regular (Møhl et al. 2000) and slow clicks (Lamoni et al. 2012). This is supported by the observed changes in the pulse structure within slow click bouts, since the click structure of sperm whales (Zimmer et al. 2005a, Zimmer et al. 2005b) and other cetaceans (Koblitz et al. 2012) is affected by the recording angle. It is thus possible that slow-clicking whales are changing their body orientation in relation to the hydrophone - possibly by rotating on their longitudinal axis on their way to the surface (Figure 3.9). If slow-clicking whales do change body orientation, the CV increase in amplitude with increasing number of slow clicks per bout in this study suggests that longer bouts are generally associated with a greater change in body orientation.

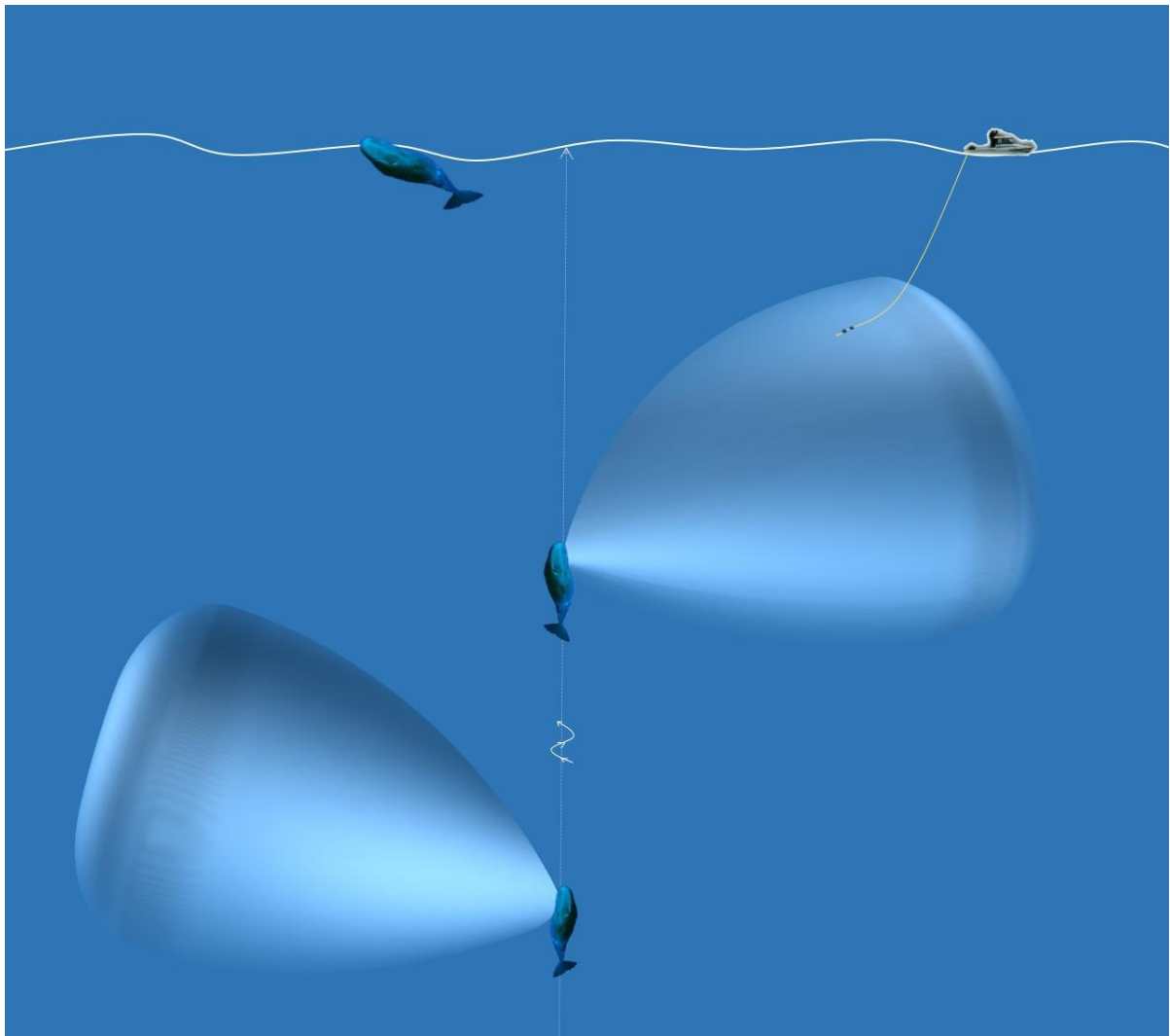


Figure 3.9– Proposed change in body orientation of slow clicking whales relative to a stationary hydrophone deployed from the research vessel. A whale slow-clicking every c. 6 s while rotating on its longitudinal axis during ascent. The laterally directed beam pattern of slow clicks depicted (horizontal cone-like structures) was inspired by Lamoni and colleagues (2012) and is a rough representation of the directionality of slow clicks. Not to scale.

Whales could be directing the beam of slow clicks, which is possibly directed laterally (Lamoni et al. 2012), and hence propagating parallel to the ocean surface and bottom towards particular target/s (Figure 3.9). An apparent small variation of the pulse structure within bouts, which suggests small changes in body orientation relative to the receiver, would hence indicate a ‘narrow’ focused use of slow clicks; whereas a high variation would be associated with a wider area covered by those slow-clicking whales (see Figure 3.8A). An alternative hypothesis may be that the whales significantly alter their waveform patterns and output levels during bouts, but this is not supported by studies of click waveform or directionality in sperm whales (Zimmer et al. 2005a, Zimmer et al. 2005b) and other cetaceans (Koblitz et al. 2012), or by observations that suggest constant apparent source levels for any given regular click series (Møhl et al. 2000), including slow clicks (Lamoni et al. 2012).

My observation that recording distances did not affect the occurrence of multiple pulses supports the idea that slow-clicking whales may be broadcasting slow click IPI-related parameters, even though these did not correlate with those IPIs of regular searching clicks. However, if whales choose broadcasting directions in proportion to the number of other whales in the area, the variation of the pulse structure within bouts found here would possibly correlate with the number of other whales in the area, which was not the case. By choosing the direction in which to slow click, whales could maintain a foraging area clear of competitors, as previously suggested (Madsen et al. 2002b), or maintain group cohesion, which could have been the case of the group of males trapped in the Scapa Flow, Orkney Islands (Goold 1999). However, directing the beam of slow clicks may also be used for broad-scale echolocation of large structures (i.e., slopes) or conspecifics (Gordon 1987, Mullins et al. 1988, Weilgart and Whitehead 1988, Whitehead 1993, Goold 1999). Spatial orientation and/or planning of subsequent dives, as previously reported to be an additional feature of regular clicks (Fais et al. 2015), should not be ruled out as a potential function of slow clicks (section 2.4.3; Chapter 2). In conclusion, the beam pattern of slow clicks and the body posture of slow-clicking whales may jointly play an important role in the effectiveness of these clicks, and may hold important information about the function/s of these so far puzzling vocalisations.

3.5. References

- Ainslie, M. A., and J. G. McColm. 1998. A simplified formula for viscous and chemical absorption in sea water. *Journal of the Acoustical Society of America* **103**(3):1671-1672.
- Antunes, R., L. Rendell, and J. Gordon. 2010. Measuring inter-pulse intervals in sperm whale clicks: consistency of automatic estimation methods. *Journal of the Acoustical Society of America* **127**(5):3239-3247.
- Backus, R. H., and W. E. Schevill. 1966. Physeter clicks. Pages 510–528 in K. S. Norris, editor. *Whales, dolphins, and porpoises*. University of California Press, Berkeley.
- Barlow, J., and B. L. Taylor. 2005. Estimates of sperm whale abundance in the northeastern temperate Pacific from a combined acoustic and visual survey. *Marine Mammal Science* **21**(3):429-445.
- Bee, M. A., and H. C. Gerhardt. 2001. Neighbour–stranger discrimination by territorial male bullfrogs (*Rana catesbeiana*): I. Acoustic basis. *Animal Behaviour* **62**(6):1129-1140.
- Beecher, M. D. 1989. Signalling systems for individual recognition: an information theory approach. *Animal Behaviour* **38**(2):248-261.
- Best, P. B. 1979. Social organization in sperm whales, *Physeter macrocephalus*. Pages 227-289 in H. E. Winn and B. L. Olla, editors. *Behavior of Marine Animals*. Springer US.
- Bogert, B. P., M. J. R. Healy, and J. W. Tukey. 1963. The quefrency analysis of time series for echoes: cepstrum, pseudo-autocovariance, cross-cepstrum and saphe cracking. Pages 209-243 in M. Rosenblatt, editor. *Proceedings of the Symposium on Time Series Analysis*. John Wiley and Sons, New York.
- Bradford, J. M. 1970. Diurnal variation in vertical distribution of pelagic copepods off Kaikoura, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **4**(4):337-350.
- Caruso, F., V. Sciacca, G. Bellia, E. De Domenico, G. Larosa, E. Papale, C. Pellegrino, S. Pulvirenti, G. Riccobene, and F. Simeone. 2015. Size distribution of sperm whales acoustically identified during long term deep-sea monitoring in the Ionian Sea. *PLoS ONE* **10**(12):e0144503.
- Charif, R. A., A. M. Waack, and L. M. Strickman. 2008. *Raven Pro 1.3 User's Manual*. The Cornell Laboratory of Ornithology, Ithaca, New York.
- Childerhouse, S. J., S. M. Dawson, and E. Slooten. 1995. Abundance and seasonal residence of sperm whales at Kaikoura, New Zealand. *Canadian Journal of Zoology* **73**(4):723-731.
- Christie, P. J., D. J. Mennill, and L. M. Ratcliffe. 2004. Pitch shifts and song structure indicate male quality in the dawn chorus of black-capped chickadees. *Behavioral Ecology and Sociobiology* **55**(4):341-348.
- Clarke, R. 1956. Sperm whales of the Azores. *Discovery Reports* XXVIII:237–298.
- Doty, G. V., and A. M. Welch. 2001. Advertisement call duration indicates good genes for offspring feeding rate in gray tree frogs (*Hyla versicolor*). *Behavioral Ecology and Sociobiology* **49**(2-3):150-156.
- Ellis, W. A. H., and F. B. Bercovitch. 2011. Body size and sexual selection in the koala. *Behavioral Ecology and Sociobiology* **65**(6):1229-1235.

- Fais, A., N. Aguilar de Soto, M. Johnson, C. Pérez-González, P. J. O. Miller, and P. T. Madsen. 2015. Sperm whale echolocation behaviour reveals a directed, prior-based search strategy informed by prey distribution. *Behavioral Ecology and Sociobiology* **69**(4):663-674.
- Fischer, J., D. M. Kitchen, R. M. Seyfarth, and D. L. Cheney. 2004. Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology* **56**(2):140-148.
- Fitch, W. T. 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America* **102**(2):1213-1222.
- Fitch, W. T., and M. D. Hauser. 2003. Unpacking “honesty”: vertebrate vocal production and the evolution of acoustic signals. Pages 65-137 in A. M. Simmons, R. R. Fay, and A. N. Popper, editors. *Acoustic Communication*. Springer, New York.
- Flewellen, C. G., and R. J. Morris. 1978. Sound velocity measurements on samples from the spermaceti organ of the sperm whale (*Physeter catodon*). *Deep Sea Research* **25**(3):269-277.
- Gaskin, D. E. 1970. Composition of schools of sperm whales *Physeter catodon* Linn. east of New Zealand. *New Zealand Journal of Marine and Freshwater Research* **4**(4):456-471.
- Gero, S., H. Whitehead, and L. Rendell. 2016. Individual, unit and vocal clan level identity cues in sperm whale codas. *Royal Society Open Science* **3**(1):150372.
- Gillespie, D., D. K. Mellinger, J. Gordon, D. McLaren, P. Redmond, R. McHugh, P. W. Trinder, X. Y. Deng, and A. Thode. 2009. PAMGUARD: Semiautomated, open source software for real-time acoustic detection and localisation of cetaceans. *Journal of the Acoustical Society of America* **125**(4):2547.
- Goold, J. C. 1999. Behavioural and acoustic observations of sperm whales in Scapa Flow, Orkney Islands. *Journal of the Marine Biological Association of the UK* **79**(3):541-550.
- Goold, J. C., J. D. Bennell, and S. E. Jones. 1996. Sound velocity measurements in spermaceti oil under the combined influences of temperature and pressure. *Deep Sea Research Part I: Oceanographic Research Papers* **43**(7):961-969.
- Gordon, J. C. D. 1987. Sperm whale groups and social behaviour observed off Sri Lanka. PhD thesis. University of Cambridge.
- Gordon, J. C. D. 1991. Evaluation of a method for determining the length of sperm whales (*Physeter catodon*) from their vocalizations. *Journal of Zoology* **224**(2):301-314.
- Growcott, A., B. Miller, P. Sirguy, E. Slooten, and S. Dawson. 2011. Measuring body length of male sperm whales from their clicks: the relationship between inter-pulse intervals and photogrammetrically measured lengths. *Journal of the Acoustical Society of America* **130**(1):568-573.
- Huggenberger, S., M. André, and H. H. A. Oelschläger. 2016. The nose of the sperm whale: overviews of functional design, structural homologies and evolution. *Journal of the Marine Biological Association of the UK* **96**(4):783-806.
- Jacobson, M. Z. 2005. Studying ocean acidification with conservative, stable numerical schemes for nonequilibrium air-ocean exchange and ocean equilibrium chemistry. *Journal of Geophysical Research: Atmospheres* **110**(D07302):1-17.

- Jaquet, N., S. Dawson, and L. Douglas. 2001. Vocal behaviour of male sperm whales: why do they click? *Journal of the Acoustical Society of America* **109**(5):2254-2259.
- Jensen, F. H., L. Bejder, M. Wahlberg, and P. T. Madsen. 2009. Biosonar adjustments to target range of echolocating bottlenose dolphins (*Tursiops* sp.) in the wild. *Journal of Experimental Biology* **212**(Pt8):1078-1086.
- Koblitz, J. C., M. Wahlberg, P. Stilz, P. T. Madsen, K. Beedholm, and H.-U. Schnitzler. 2012. Asymmetry and dynamics of a narrow sonar beam in an echolocating harbor porpoise. *Journal of the Acoustical Society of America* **131**(3):2315-2324.
- Lamoni, L. U., R. Antunes, P. J. Miller, and P. L. Tyack. 2012. "Boy-talk": acoustic characterisation of sperm whale slow clicks in a male-only high latitude feeding ground. University of St Andrews.
- Lettevall, E. 1993. Estimating the length of sperm whales (*Physeter macrocephalus*) off northern Norway using a photo-telemetric technique. MSc thesis. Göteborg University.
- Lettevall, E., C. Richter, N. Jaquet, E. Slooten, S. Dawson, H. Whitehead, J. Christal, and P. M. Howard. 2002. Social structure and residency in aggregations of male sperm whales. *Canadian Journal of Zoology* **80**(7):1189-1196.
- Lieberman, P. 1984. The biology and evolution of language. Harvard University Press, Cambridge.
- Lurton, X. 2002. An introduction to underwater acoustics: principles and applications. Springer -Verlag, 347 pp.
- Madsen, P. T., R. Payne, N. U. Kristiansen, M. Wahlberg, I. Kerr, and B. Møhl. 2002a. Sperm whale sound production studied with ultrasound time/depth-recording tags. *Journal of Experimental Biology* **205**(Pt13):1899-1906.
- Madsen, P. T., M. Wahlberg, and B. Møhl. 2002b. Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and communication. *Behavioral Ecology and Sociobiology* **53**(1):31-41.
- Marcoux, M., H. Whitehead, and L. Rendell. 2006. Coda vocalizations recorded in breeding areas are almost entirely produced by mature female sperm whales (*Physeter macrocephalus*). *Canadian Journal of Zoology* **84**(4):609-614.
- Mendes, S., N. Jason, R. J. Reid, A. F. Zuur, and G. J. Pierce. 2007. Stable carbon and nitrogen isotope ratio profiling of sperm whale teeth reveals ontogenetic movements and trophic ecology. *Oecologia* **151**(4):605-615.
- Miller, B. S. 2010. Acoustically derived growth rates and three-dimensional localisation of sperm whales (*Physeter macrocephalus*) in Kaikoura, New Zealand. PhD thesis. University of Otago.
- Miller, B. S., A. Growcott, E. Slooten, and S. M. Dawson. 2013. Acoustically derived growth rates of sperm whales (*Physeter macrocephalus*) in Kaikoura, New Zealand. *Journal of the Acoustical Society of America* **134**(3):2438-2445.
- Miller, P. J. O., M. P. Johnson, and P. L. Tyack. 2004. Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. *Proceedings of the Royal Society B: Biological Sciences* **271**(1554):2239-2247.

- Møhl, B. 2001. Sound transmission in the nose of the sperm whale *Physeter catodon*. A post mortem study. *Journal of Comparative Physiology A* **187**(5):335-340.
- Møhl, B., M. Wahlberg, P. T. Madsen, A. Heerfordt, and A. Lund. 2003. The monopulsed nature of sperm whale clicks. *Journal of the Acoustical Society of America* **114**(2):1143-1154.
- Møhl, B., M. Wahlberg, P. T. Madsen, L. A. Miller, and A. Surlykke. 2000. Sperm whale clicks: directionality and source level revisited. *Journal of the Acoustical Society of America* **107**(1):638-648.
- Morton, E. S. 1986. Predictions from the ranging hypothesis for the evolution of long distance signals in birds. *Behaviour* **99**(1):65-86.
- Mullins, J., H. Whitehead, and L. S. Weilgart. 1988. Behaviour and vocalizations of two single sperm whales, *Physeter macrocephalus*, off Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences* **45**(10):1736-1743.
- Nishiwaki, M., S. Ohsumi, and Y. Maeda. 1963. Change of form in the sperm whale accompanied with growth. *Scientific Reports of the Whales Research Institute* **17**:1-14.
- Norris, K. S., and G. W. Harvey. 1972. A theory for the function of the spermaceti organ of the sperm whale (*Physeter catodon* L.). *NASA Special Publication* **262**:397-417.
- Ohsumi, S. 1971. Some investigations on the school structure of sperm whale. Tokyo.
- Oliveira, C., M. Wahlberg, M. Johnson, P. J. O. Miller, and P. T. Madsen. 2013. The function of male sperm whale slow clicks in a high latitude habitat: communication, echolocation, or prey debilitation? *Journal of the Acoustical Society of America* **133**(5):3135-3144.
- Pfefferle, D., and J. Fischer. 2006. Sounds and size: identification of acoustic variables that reflect body size in hamadryas baboons, *Papio hamadryas*. *Animal Behaviour* **72**(1):43-51.
- Pinela, A. M., S. Quéroutil, S. Magalhães, M. A. Silva, R. Prieto, J. A. Matos, and R. S. Santos. 2009. Population genetics and social organization of the sperm whale (*Physeter macrocephalus*) in the Azores inferred by microsatellite analyses. *Canadian Journal of Zoology* **87**(9):802-813.
- Reby, D., and K. McComb. 2003. Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour* **65**(3):519-530.
- Rhineland, M. Q., and S. M. Dawson. 2004. Measuring sperm whales from their clicks: stability of interpulse intervals and validation that they indicate whale length. *Journal of the Acoustical Society of America* **115**(4):1826-1831.
- Rice, D. W. 1989. Sperm whale, *Physeter macrocephalus* (Linnaeus, 1758). Pages 177-233 in S. H. Ridgway and R. Harrison, editors. *Handbook of Marine Mammals*. Academic Press, London, UK.
- Shapiro, S. S., and M. B. Wilk. 1965. An analysis of variance test for normality (complete samples). *Biometrika* **52**(3-4):591-611.
- Teloni, V., W. M. X. Zimmer, M. Wahlberg, and P. T. Madsen. 2007. Consistent acoustic size estimation of sperm whales using clicks recorded from unknown aspects. *Journal of Cetacean Research and Management* **9**(2):127-136.

- Tyack, P. L., and C. W. Clark. 2000. Communication and acoustic behavior of dolphins and whales. Pages 156-224 in W. W. L. Au, A. N. Popper, and R. R. Fay, editors. Hearing by whales and dolphins. Springer, New York.
- Vannoni, E., and A. G. McElligott. 2008. Low frequency groans indicate larger and more dominant fallow deer (*Dama dama*) males. PLoS ONE **3**(9):e3113.
- Wahlberg, M. 2002. The acoustic behaviour of diving sperm whales observed with a hydrophone array. Journal of Experimental Marine Biology and Ecology **281**(1):53-62.
- Watkins, W. A., and W. E. Schevill. 1977. Sperm whale codas. Journal of the Acoustical Society of America **62**(6):1485-1490.
- Weilgart, L. S., and H. Whitehead. 1988. Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). Canadian Journal of Zoology **66**(9):1931-1937.
- Whitehead, H. 1993. The behaviour of mature male sperm whales on the Galápagos Islands breeding grounds. Canadian Journal of Zoology **71**(4):689-699.
- Whitehead, H. 2003. Sperm whales: social evolution in the ocean. University of Chicago Press.
- Zimmer, W. M. X., P. T. Madsen, V. Teloni, M. P. Johnson, and P. L. Tyack. 2005a. Off-axis effects on the multipulse structure of sperm whale usual clicks with implications for sound production. Journal of the Acoustical Society of America **118**(5):3337-3345.
- Zimmer, W. M. X., P. L. Tyack, M. P. Johnson, and P. T. Madsen. 2005b. Three-dimensional beam pattern of regular sperm whale clicks confirms bent-horn hypothesis. Journal of the Acoustical Society of America **117**(3):1473-1485.

4. Synchronised surfacing: codas, slow clicks and long-term bonds

Abstract

Sperm whale (*Physeter macrocephalus*) social structure is highly complex and not yet well understood. Different sexes show different geographic distributions, where females live in long-term social units in tropical and temperate waters, while males disperse towards higher latitudes. Male-only foraging grounds include areas termed “aggregations” where both independent mature males and “bachelor groups” can be found. Codas are stereotyped patterns of clicks used for communication, and have almost exclusively been recorded from long-term female social units. Coda repertoires are thought to be culturally transmitted and populations have been divided according to their acoustic clan. Independent males have rarely been associated with coda production; however, they use a click type not used by females, the slow clicks. Slow clicks are thought to be a form of long-range communication that may have different functions depending on the social context. As males are rarely observed in social contexts, slow clicking seems to be primarily associated with competition for females in breeding grounds, and for foraging space in male-only habitats, although social cohesion has also been suggested as a function. Here, I describe a rare observation of physical and vocal interaction between two males, within a high latitude male-only foraging ground. During a complete dive cycle off Kaikoura, the pair of whales coordinated at the surface and produced codas, slow clicks and coda-creaks (fast series of clicks typically associated with socialising females), while actively foraging. I found stereotyped patterns of clicks, commonly termed codas, made using clicks with spectral and waveform characteristics of slow clicks, which I termed ‘slow click codas’. ‘Slow click codas’, which were produced in conjunction with ‘traditional’ codas, were found in a sequence prior to the whales surfacing together. These were longer than traditional codas, with lower centre frequency and higher relative amplitude. This observation may suggest a form of communication between the pair of males, questioning the idea that male sperm whales are ‘non-social’ animals, while highlighting the lack of knowledge about male-male vocal communication.

4.1. Introduction

Male sperm whales (*Physeter macrocephalus*) are born in social units comprised of adult females and immatures, where most females spend their lives in the same unit and show philopatry within their home range in tropical and subtropical waters (Best 1979, Engelhaupt et al. 2009, Lyrholm and Gyllenstein 1998, Mesnick 2001, Whitehead 1987). As juveniles, males disperse towards higher latitudes and are thought to live in bachelor groups for a few years, after which they are mostly seen alone (Best 1979, Pinela et al. 2009). The geographical segregation of sexes seems to result in changes to male social (Lettevall et al. 2002, Rice 1989) and foraging (Teloni et al. 2008) behaviour, diet (Gaskin and Cawthorn 1967, Mendes et al. 2007), and movement patterns, which may include long-distance migrations when returning to female grounds to mate (Ivashin 1967, Steiner et al. 2012). Some of these aspects, such as whether they are social after leaving their natal units, their movement patterns during dispersal, or the periodicity with which they return to female grounds for mating, are poorly understood (Lettevall et al. 2002, Whitehead 2003), despite being essential information to improve management and protection of sperm whale populations.

Female long-term social bonds can last decades (Gero et al. 2015, Gero et al. 2014), and may increase offspring survival by alloparental care (Gero et al. 2009, Gordon 1987). The basic level of female social structure is the social ‘unit’; temporary associations of social units are termed ‘groups’ (Whitehead et al. 1991). Females from units and groups, including juveniles of both sexes, coordinate between well-defined foraging, and socialising (including resting and travelling) periods (Whitehead 2003). During foraging (about two thirds of the time), social units may spread over several miles in formation, with individuals diving repeatedly (Whitehead 2003). During non-foraging times, the whales often cluster at or near the surface, where vocal communication and physical activities may take place (Best 1979, Gordon and Steiner 1992, Watwood et al. 2006, Whitehead 2003, Whitehead et al. 1989).

Sperm whales produce stereotyped patterns of communication clicks, termed ‘codas’ (Norris 1966, Schulz et al. 2011, Watkins and Schevill 1977, Weilgart and Whitehead 1993). Codas have been mostly studied from socialising social units and groups (Drouot et al. 2004b, Marcoux et al. 2006, Moore et al. 1993, Rendell and Whitehead 2003a, Rendell and Whitehead 2003b, Watkins and Schevill 1977, Weilgart and Whitehead 1993, Whitehead and Weilgart 1991). Coda clicks show low directionality, more pronounced secondary pulses and a centre frequency (the frequency that divides the spectrum in two parts of equal energy) between 7-9 kHz (Madsen et al. 2002a). Despite various studies since codas were first observed in

1966 by Norris, the actual message carried by codas is unknown (Whitehead 2003). Marcoux et al. (2006) noticed that codas within groups were almost exclusively produced by adult females and suggests that they may be important in forming and maintaining bonds. Groups vary in their use of different coda types (Weilgart and Whitehead 1997) and coda repertoires reveal a higher level of social structure, identified as ‘vocal clans’, similar to the ‘acoustic clans’ of killer whales, and probably resulting from cultural transmission (Rendell and Whitehead 2003b). Vocal clans result in units preferring to form groups with other units of their own acoustic clan (Rendell and Whitehead 2003b). In addition, females seem to recognise each other by showing individual preferences within, and across long-term social units throughout decades (Gero et al. 2015).

Although it has been proposed that codas may be individually distinctive (Watkins et al. 1985, Watkins and Schevill 1977), there are more individuals than different number of codas within regions, individuals produce more than one coda type and coda types are shared by different individuals, which challenges the individual ‘signature’ hypothesis (Moore et al. 1993, Weilgart and Whitehead 1993). However, a more recent study by Antunes et al. (2011) found that some individuals from a single social group could be individually identified by the way they execute a certain coda type, the ‘5 Regular’, composed of five regularly inter-spaced clicks, by analysing the absolute inter-click interval (ICI) differences produced by different individuals.

‘Coda-creaks’ (Weilgart 1990) or ‘Chirrup’ (Gordon 1987) are different terms used for high-rate echolocation clicks used during socialising periods, otherwise ‘creaks’ (or ‘buzzes’) are associated with short-range echolocation prior to prey capture during foraging (Gordon 1987, Miller et al. 2004). Coda-creaks have shorter duration (0.77 s on average; (Weilgart 1990)) than foraging creaks (length ca. 5 to 44 s, see table 5.7; (Whitehead 2003).

Slow clicks are a male-only vocalisation (Weilgart and Whitehead 1988). They may have a distinctive metallic-like sound, long ICIs of several seconds and a low frequency emphasis, roughly between 2–4 kHz (Madsen et al. 2002b). They are thought to have a communicative function that has been attributed to acoustic display between males within breeding grounds (Gordon 1987, Weilgart and Whitehead 1988) and practicing of courtship displays, or acoustic display in competition for food at higher latitude male-only foraging grounds (Madsen et al. 2002b, Mullins et al. 1988). Within male-only grounds slow clicks are produced in bouts with long inter-click intervals of 4 to 10 seconds, typically at the end of dives (Jaquet et al. 2001, Oliveira et al. 2013).

Young males form size-restricted “bachelor schools” (Best 1979, Gaskin 1970), which coordinate over large areas (Best 1979), although males do not appear to maintain the same social organisation of females. Long-term bonds have never been observed between independent males, but they do share feeding grounds at higher latitudes. These so-called ‘aggregations’ (Lettevall et al. 2002), include the Kaikoura canyon, in New Zealand (Dawson et al. 1994). Aggregations have been observed consistently moving together (Caldwell et al. 1966) for distances up to 50 km (Christal and Whitehead 1997). Within aggregations, males are rarely seen clustering at the surface, and codas are very seldom heard (Gordon et al. 1992, Lettevall et al. 2002, Madsen et al. 2002b), leading to uncertainty about intentional social cohesion among males, which suggests solitary or potentially competitive foraging behaviour among male-only grounds at high latitudes (Madsen et al. 2002b). Except for one study on non-solitary males conducted in the Mediterranean Sea by Frantzis and Alexiadou (2008), which showed an association between coda types and behavioural contexts, there are no studies of coda production focused on ‘independent’ male sperm whales. Judging by the scarcity of codas produced by males, they possibly rely less on these signals than females, yet the regular use of slow clicks in male-only grounds may potentially play a role in male social organisation (Oliveira et al. 2013).

Here, I describe a rare occurrence where two consecutive synchronised surfacings were performed by two male sperm whales off Kaikoura. Coda and slow clicks produced by the pair of whales were described in terms of their temporal patterns, centre frequency and relative amplitude.

4.2. *Methods*

4.2.1. *Data collection and analysis*

Acoustical and visual data from two male sperm whales performing two consecutive synchronised surfacings were collected on the 12th of September 2009 in the Kaikoura canyon, south of the Kaikoura peninsula, on the East coast of South island of New Zealand (see Figure 2.1 in Chapter 2). Data collection, animal identification and technical details of the acoustic hardware, software and settings applied (including high-pass filtering) were as described in detail in sections 2.2.1 - 2.2.4 in Chapter 2. A complete dive cycle (hereinafter dive) was defined as the time between two consecutive fluke-up events (start of dive) from the same animal (see Figure 2.2 in Chapter 2).

Acoustic data was manually audited using Pamguard (Gillespie et al. 2009) and Rainbowclick (Gillespie 1997) software, to filter and label different clicks from individual whales. The click types labelled here were regular clicks (long-range echolocation foraging clicks), creak clicks (feeding-indicator clicks), slow clicks and coda clicks. The centre frequency (the frequency that divides the spectrum in two parts of equal energy) of coda and slow clicks were measured using Raven Pro 1.3 (Charif et al. 2008). The information associated with clicks was stored on a Microsoft Access Database and included a link to the whale ID, time, bearing of clicks, and their relative amplitude.

Codas were defined as repeated stereotyped short series of 2-43 clicks, adapted from Watkins and Schevill (1977). A high noise ratio margin facilitated click identification and labelling. Slow clicks were distinguished from regular clicks by their $ICI > 2.5$ s (as opposed to $ICI \leq 2$ s), except for metallic-like clicks, as described by Gordon (1987) and Jaquet and colleagues (2001), that showed a clear centre frequency between 2–4 kHz (compared to about 15 kHz for regular clicks and 2–4 kHz for slow clicks (Madsen et al. 2002b)). Metallic-like clicks were visually confirmed by waveform display as slow clicks (Madsen et al. 2002b). Slow click ‘events’ were defined as either bouts of slow clicks with ICIs between 2.5-10 s, or single slow clicks more than 10 s apart. Creaks were defined as high-repetition rate click series with inter-click intervals ≤ 0.1 s, as defined by (Teloni et al. 2008, Whitehead and Weilgart 1990).

I classified codas according to their temporal patterns (Weilgart and Whitehead 1997) excluding the common procedure of standardising codas using their ICI divided by the coda duration (Weilgart and Whitehead 1997). This was because I had a small number of codas

(n=35) and observed patterns (9). I grouped codas as demonstrated in the following example. A coda termed 1+3+1 indicates that it contains a total of 5 clicks, where the sign '+' separates single clicks, clusters of closely spaced clicks, or clicks with similar ICIs within the coda (i.e., when the ICI between clustered clicks does not exceed 1.5 times the length of other ICIs within a cluster). Coda duration was the time between the first and last click within a coda and inter-coda interval was defined as the time between the last click of a coda and the first click of the next coda. Coda session was defined as groups of codas within different dive phase: 'beginning' (up to 8 min after start of dive), 'middle' (neither in the 'beginning' nor in the 'end' phases) and 'end' of dive phase (within the last 8 min of the dive before surfacing).

Coda-creaks have a similar repetition rate to feeding creaks (Whitehead 2003) and were distinguished by their shorter duration of 2.15 s average for the two coda-creaks detected, compared with a mean creak duration of 16.5 (SD=8.4) found from the analysis of 741 creaks from Chapter 2.

I compared the centre frequency means from different click types using t-tests with normally distributed samples and compared mean centre frequency using Mann-Whitney U Tests for samples that did not follow a normal distribution.

4.3. Results

4.3.1. Available data

In addition to the dives analysed here involving whale ID1 (hereinafter whale 1) and whale ID35 (hereinafter whale 35), another forty-three dives from whale 1 and fifty-three dives from another 13 individual whales and their corresponding vocalisations were available from Chapter 2. During dives analysed for Chapter 2, whale 1 never surfaced with other whales, and its vocal repertoire consisted of ‘regular clicks’, ‘creak clicks’ and ‘slow clicks’. No ‘coda clicks’ had been identified from whale 1.

Whale 1 and whale 35 had been previously photographed clustering at the surface on the 28 November 2006 in the same general area. This information was acquired during field work for a master thesis by Van der Linde (2010).

4.3.2. Brief description of the field observation

On the 12th of September 2010, while visually and acoustically tracking whale 1, another (whale 35) surfaced, unusually, within about a body length from the focal whale (whale 1). Codas and slow clicks were heard shortly prior to the whales surfacing together, and slow clicks continued to be heard about every 8 s during the first min while the animals were at the surface. Slow clicks are commonly heard off Kaikoura from foraging animals just prior to surfacing, and occasionally at the surface (see Chapter 2), although codas are seldom heard. The two whales surfaced for about 6 min, after which they dived side by side almost simultaneously. Shortly after fluke up (diving), 10 codas were heard within 2 min and 15 s, precisely the same length of time used for 16 coda sequences heard before the animals were first spotted at the surface, although different coda types were heard this time. Approximately half way through the dive, 2 coda-creaks were heard, and towards the end of the dive another sequence of 7 codas and slow click bouts were heard. The whales then surfaced side-by-side for the second time, in silence, and after about 9 min they fluked up again. One additional coda, consisting of 3 regularly spaced clicks, was heard shortly after the pair of whales dived for the second time. This additional coda was excluded from the analysis as I did not have recordings for the complete dive. On the subsequent surfacing, whale 35 was seen alone. A schematic representation of codas types and where they occurred within the two dives analysed can be seen in Figure 4.1.

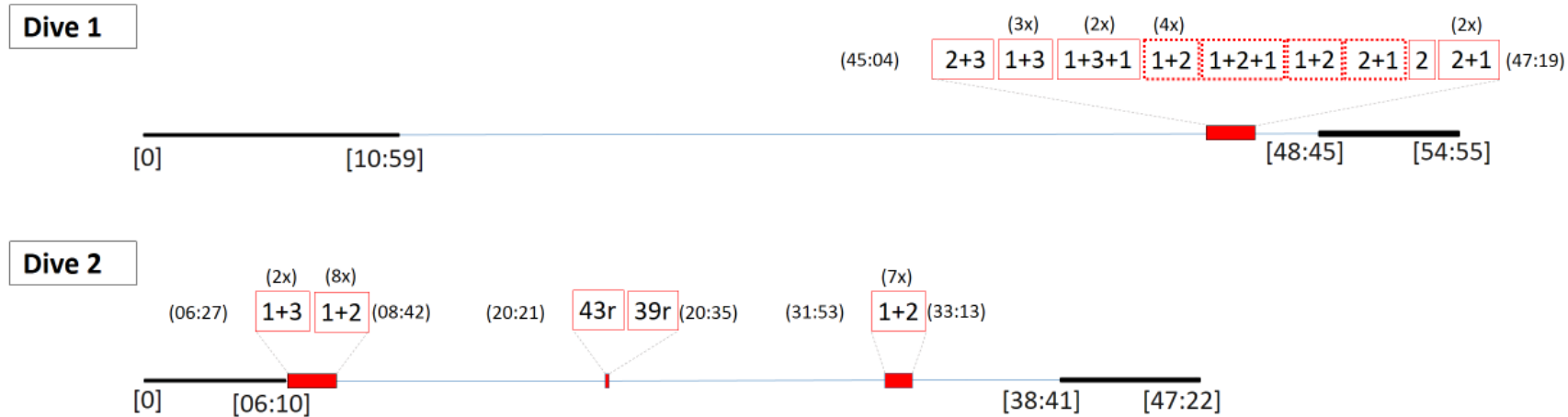


Figure 4.1 – Timing of codas within two consecutive dives (Dive 1 and Dive 2), from which dive 2 showed the same pair of male sperm whales diving and surfacing together. Horizontal lines show time (mm:ss), where black bold represents time spent at the surface between dives. Red rectangles on timeline show when coda sessions and the two coda-creaks (43r and 39r) took place and red text-boxes display the coda type in the observed order with numbers between brackets on top indicating the number of repetitions of the same coda type. Dotted red text-boxes indicate codas composed of clicks with slow click characteristics (see section 4.3.5). As these are sequential dives, the second surfacing of dive 1 ([48:45]-[54:55]) is the same as the first surfacing from dive 2 ([0]-[06:10]).

4.3.3. Overview

The analysis of the acoustic recordings revealed 35 codas, 66 slow clicks and 17 creaks. Codas were labelled in 9 distinct ‘coda types’, including 7 codas and 2 coda-creaks. Codas from the whales in proximity to each other, assumed to be the pair of whales previously clustering at the surface (hereinafter ‘whales’ or the ‘pair of whales’), were produced either at the very beginning, or close to the end of dives, except for the two coda-creaks (43r and 39r), which were detected approximately in the middle of dive two (Figure 4.1). The additional coda composed of 3 regularly spaced clicks heard shortly after the pair of whales dived for the second time was not included in Figure 4.2, where the average time between clicks of the same coda type, coda types and the number of codas are shown. Due to the proximity of the pair of whales to one another (confirmed by the very similar bearings of clicks relative to the hydrophones), it was not always possible to link vocalisations to individual whales; neither could I confirm coda nor slow click exchange, but rather its presence. It was occasionally possible, however, to distinguish the whale producing codas from the whale producing regular or slow clicks by the different bearings of clicks displayed simultaneously.

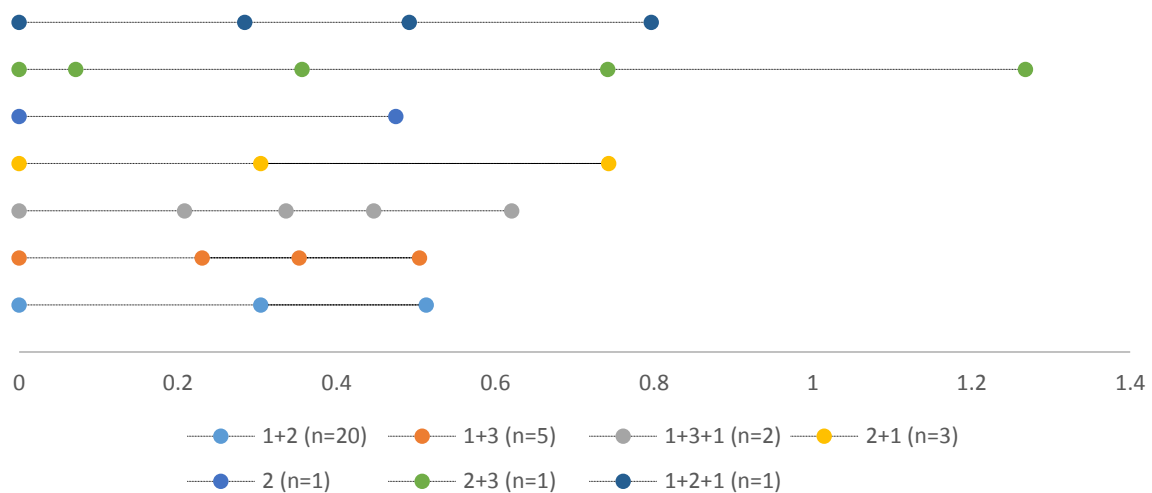


Figure 4.2 – Average time between clicks (ICIs) for the same coda types displayed on a time line shown in seconds. Each dot represents a click and lines represent a coda type composed of different number of clicks with different time patterns.

Slow clicks were present in both ends of the dives, as single clicks, long bouts, and apparently used in stereotyped series of clicks (see section 4.3.5). Additionally, the recordings

contained creaks from both whales. Five creaks were identified on dive one and 12 on dive two. Even though I could not distinguish which whale was creaking, it was sometimes possible to confirm simultaneous creaks from the two whales in proximity to each other, indicating that during dive 2 the pair of whales was actively foraging.

4.3.4. *Coda-creaks*

The two coda-creaks were longer (2.4 s and 1.9 s respectively) than the codas (< 0.9 s) and had a higher number of clicks; while codas had a maximum of five clicks, the two coda-creaks had 43 and 39 clicks, respectively. The mean ICI (0.05 s; SD=0.02) within coda-creaks was very consistent. Coda-creaks were detected during a period where both whales stopped regular clicking, and between two creaks from either whales. The first coda-creak overlapped with a regular click train from the other whale, continued vocalising using coda-creaks and showed a constant ICI averaging 0.27 s (SD=0.01) suggesting an approximate scanning distance of 206 m. Coda-creaks were not displayed in Figure 4.2, as these are considered to have a different (although unclear) function to the most studied stereotyped patterns of clicks (i.e., codas) (Gordon 1987, Weilgart 1990).

4.3.5. *Spectral frequency analysis of coda and slow clicks*

Slow click centre frequency is between 2–4 kHz (Madsen et al. 2002b), while that of codas is between 7-9 kHz (Madsen et al. 2002a). Slow clicks have a higher relative amplitude than coda clicks (Whitehead 2003). During audio and visual analysis, some codas appeared to be comprised of clicks with spectral frequency characteristics of slow clicks. I called these ‘slow click codas’ (hereafter SCcodas). Clicks within SCcodas (

Figure 4.3B) showed lower frequency and a very different waveform structure compared with all other codas (

Figure 4.3A), and similar to those of slow clicks (

Figure 4.3C).

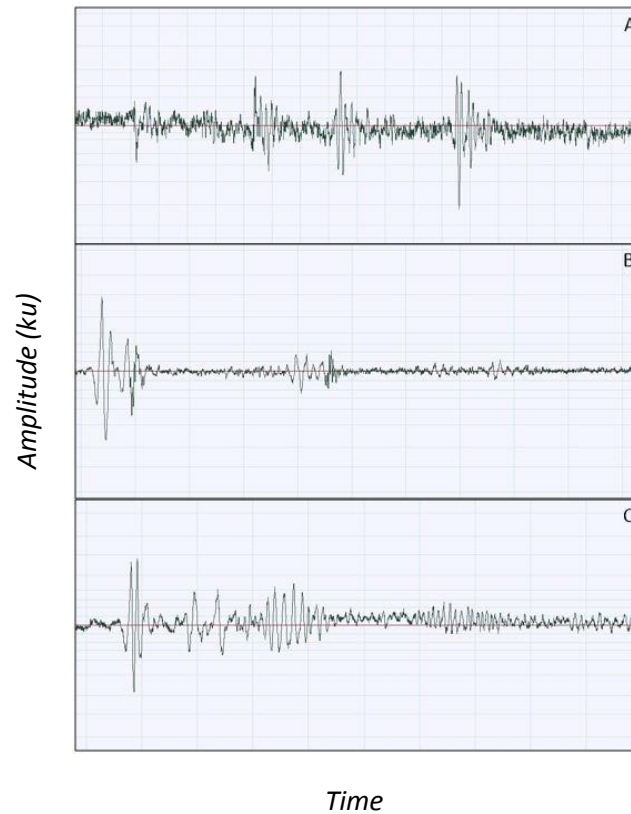


Figure 4.3 – Representative waveforms of (A) coda click with a CF=4687.5 Hz; (B) ‘slow click coda’ with a CF=3562.5 Hz; (C) ‘slow click’ with a CF=3375 Hz. Window size is approximately 20 ms.

The waveform shown in

Figure 4.3A, from a click that is part of a coda sequence, shows several pulses above the background noise. The click waveform structure matches those displayed in Madsen et al. (2002a) and in Whitehead (2003), but the decay rate (peak amplitude) between successive pulses within the clicks shown by these authors looks almost opposite to the one seen here, where the amplitude of the pulses seems to increase.

I compared the centre frequency and relative amplitude of SCcodas with the remaining codas, apparently the most common known codas, that I termed ‘coda codas’ (hereafter CCodas), and with slow clicks. This analysis was only performed for dive 1 because SCcodas were only present at the ‘end’ phase of this dive. Table 4.1 shows a summary of results between the three click types, and Table 4.2 summarises their characteristics.

*Table 4.1 – Results of t-tests (*Mann–Whitney U test) comparing centre frequency and relative amplitude means between coda codas (CCodas), slow click codas (SCcodas) and slow click.*

Centre frequency	Df	t/W	p-value	Relative amplitude	Df	t/W	p-value
CCodas vs. SCcodas	40.1	11.8	<0.001	CCodas vs. SCcodas	50.1	-12.7	<0.001
SCcodas vs. Slow clicks*	44	118	0.001	SCcodas vs. Slow clicks	41.5	1.3	0.209
CCodas vs. Slow clicks*	57	809	<0.001	CCodas vs. Slow clicks	43.6	-9.3	<0.001

CCodas showed a significantly higher mean centre frequency compared to that of SCcodas. Similarly, the centre frequency of SCcodas and CCodas compared with slow clicks were significantly different (Table 4.1 and Table 4.2), where SCcodas showed lower mean centre frequency than slow clicks. In terms of the mean relative amplitude, SCcodas were significantly higher than CCodas, but not different from slow clicks. CCodas also showed lower relative amplitude compared to slow clicks (Table 4.1). Table 4.2 below shows the mean centre frequency values for the different click types.

Table 4.2 – Mean values for centre frequency and relative amplitude of different click types. See text for click type definitions.

Click type	n	Centre frequency (Hz)	Relative amplitude (Db)
CCodas	35	6053.6	144.5
SCcodas	22	2761.4	160.0
Slow clicks	24	3210.9	158.1

SCcodas were preceded by a series of six codas (Figure 4.1) and two slow clicks displayed at the same bearing (slow clicks from the top Figure 4.4). Between the fourth and the fifth coda prior to the SCcodas, what appeared to be a slow click bout from a distant whale (not otherwise noticed) was detected and contained at least 4 clicks from which the ICIs of the first two measured 5.7 and 6 s respectively.

4.3.6. 'Coda codas' and 'slow click codas'

Based on the differences between CCodas and SCcodas (section 4.3.5), I analysed coda duration, inter-coda interval, and the dive phase they were observed in for the two groups of codas separately to highlight their frequency of occurrence and to distinguish coda types used among the two groups (Table 4.3).

Table 4.3 – Coda types and number of codas per coda type based on 'coda codas' (CCodas) and 'slow click codas' (SCcodas). See text for definitions.

Coda type	No. of CCodas	No. of SCcodas	Total
2	1	0	1
1+2	15	5	20
1+3	5	0	5
1+2+1	0	1	1
1+3+1	2	0	2
2+1	2	1	3
2+3	1	0	1
Total	26	7	33

CCodas represented 26 of the 33 (78.8%) codas detected (Table 4.3). Of a total of seven different coda types, four were exclusively CCodas, one was exclusively SCcodas and the remaining two coda types (1+2 and 2+1) were used both in CCodas and in SCcodas. The most common coda type was the 1+2 (n=20) that was present in all coda sequences detected, both at the beginning and at the end phases of dives (Figure 4.1). When considering both groups, codas made of three clicks were the most common (23) followed by the four and five click

codas (6 and 3 times, respectively). SCcodas were only produced just before the whales surfaced, corresponding to the same dive phase of slow clicks bouts found in Chapter 2. Coda duration was significantly longer for SCcodas than for CCodas ($t = -3.35$, $p = 0.009$, $Df = 8.2$), although the ICI within codas was not different between the two groups ($W = 61$, $p = 0.693$, $Df = 108$).

4.3.7. *Slow clicks and codas*

Apart from SCcodas, there were 24 slow clicks across five events (each containing 1-11 clicks) in dive one and 42 slow clicks across four events containing 4-18 clicks each in dive two. The mean number of slow clicks per event was 4.8 (SD=4.4) for dive 1 and 10.5 (SD=7) for dive 2. ICI within slow click bouts varied between 4.1-6.8 s (Table 4.4). Both dives analysed here showed more slow clicks per event compared with the average found from ninety-four dives analysed for Chapter 2 (mean 3.6; SD=2.2).

Table 4.4 – Summary table of slow click (SC) events for two dives of associating male sperm whales. Standard deviation presented when $N > 2$.

Dive	SC Events	No of clicks	Mean ICI (s) per SC event
1	1	2	6.5
1	2	1	NA
1	3	8	4.1 (SD=3)
1	4	11	7.5 (SD=1)
1	5	2	6.9
2	1	18	6.7 (SD=0.3)
2	2	15	6.7 (SD=0.8)
2	3	5	6.4 (SD=0.2)
2	4	4	6.8 (SD=0.3)

Series of codas were consistently close or overlapped with bouts of slow clicks in both dives (Figure 4.4). The closest temporal distance between a coda and a slow click throughout

my observations was 0.072 s; occurring between the second coda click and a slow click on the last coda (seen at the bottom of Figure 4.4).

SCcodas were at times alternated with either single slow clicks or bouts of slow clicks with ICIs around 2.5 s, and followed by the only 2 click coda found.

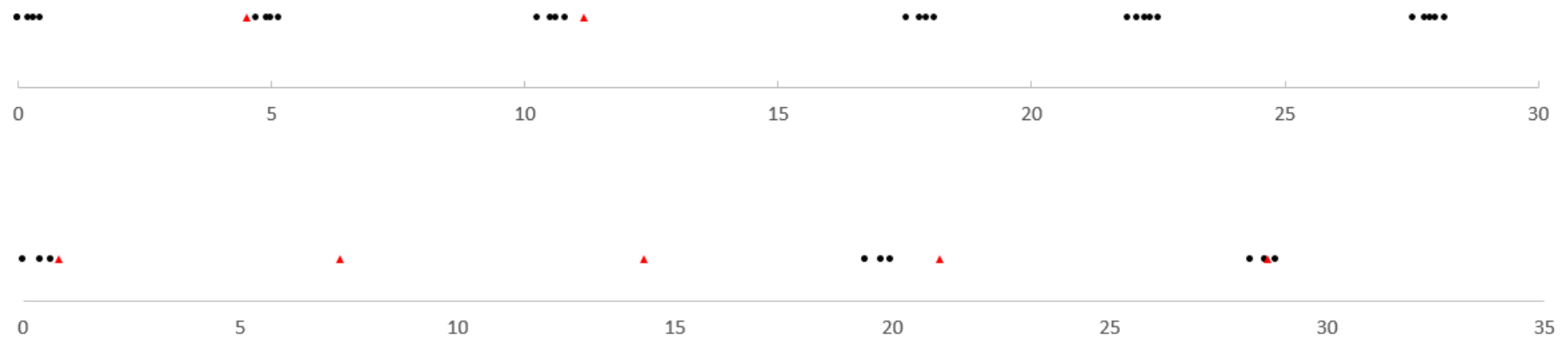


Figure 4.4 – Overlap of a coda series (black dots) and a slow click bout (red triangles) observed at the ‘end’ phases of dive 1 (top) and dive 2 (bottom). Time line is displayed in seconds.

4.3.8. *Coda matching*

Codas in this study were matched with those recorded from other geographical areas (Table 4.5). The most common coda found here (1+2) matched codas found on the Galápagos Archipelago and Tonga, whereas the two click coda (2) and the 1+3+1 did not find a match.

Table 4.5 – Studies and geographical areas matches for codas found in this study.

Codas in this study	Coda matching/geographical areas
2 (n=1)	No matches
1+2 (n=20)	1+2 from “short” and “++1/+1+1” clans; (Rendell and Whitehead 2003b) / Galápagos Archipelago and Tonga respectively
2+1 (n=3)	2+1; (Amano et al. 2014), 2+1 from "short" and “++1/+1+1” clans; (Rendell and Whitehead 2003b), 2+1 (Gordon 1987) / Kumano Coast and Galápagos Archipelago and Sri Lanka respectively
1+3 (n=5)	1+3 from “short” and “4+” clans; (Rendell and Whitehead 2003b) / Galápagos Archipelago and all regions from the South Pacific respectively
1+2+1 (n=1)	1+2+1; (Amano et al. 2014), 1+2+1 from “short”, “++1/+1+1”, “4+” and “regular” clans; (Rendell and Whitehead 2003b) / Kumano Coast, Galápagos Archipelago and Tonga
1+3+1 (n=2)	No matches
2+3 (n=1)	coda "#55"; (Antunes 2009), possibly coda “2+1+1+1”; (Weilgart and Whitehead 1997) and “2+2+1”; (Amano et al. 2014) / Sargasso’s Sea, Kumano Coast and Ogasawara Islands

4.4. *Discussion*

4.4.1. *General*

Of the many acoustic studies on sperm whales off Kaikoura (Gordon et al. 1992, Jaquet et al. 2001, Jaquet et al. 2000, Markowitz et al. 2011, Miller 2010, Miller et al. 2013a, Miller et al. 2013b, Richter et al. 2006, Richter et al. 2003), only two have reported the use of codas. Gordon et al. (1992) heard codas on two out of 40 days of data collection, while Miller (2010) mentioned hearing codas on two separate occasions, but neither confirmed that codas had been produced by males. I recorded codas in only about four of 100 days of data collection (numbers probably underestimated), supporting the notion that codas are rarely heard in Kaikoura.

The two whales studied here (ID 1 and 35) were confirmed males based on the estimated total body length of whale 1 made in Chapter 3. In addition, the same animals had been previously studied in this male-only foraging ground on different occasions (Whale ID NN20 and HL140 respectively, in Dawson et al. 1994, and Miller et al. 2013b). Therefore it is possible to confirm that the codas observed here were produced by males.

Due to their scarcity, male-produced codas have not been investigated in detail except for a study on “non-solitary” males from the Mediterranean (Frantzis and Alexiadou 2008). Here, the population is found isolated from the Atlantic ocean (Drouot et al. 2004a) and under human-related disturbance (David 2002, De Stephanis et al. 2013, Roberts 2003). In addition, the relative narrow latitude range of the Mediterranean may influence the movements and social habits of dispersing males, and caution should be applied when comparing this population with those from open oceans (Drouot-Dulau and Gannier 2007).

Lettevall and colleagues (2002) used long-term datasets to investigate the preferred companionship and long-term associates between male sperm whales from four widespread geographical areas, including Kaikoura, but found no evidence of preferred companionship or long-term associations between individuals. However, they reported two whales from Kaikoura (different individuals from those found in this study) clustering at the surface on two consecutive dives, and during a single surfacing three days later, which before the present study was the longest time between observations of associated male individuals. The current study, based on two consecutive surfacings of the same pair of whales off Kaikoura, includes recordings with communication clicks (i.e. codas) and slow clicks.

Female sperm whales maintain bonds between individuals in social units, and show individual preferences within and across groups that can last decades (Gero et al. 2015).

Although sexually mature males are thought to avoid one another in breeding grounds (Whitehead 1993), after dispersal they undergo long-distance migrations when returning to low-latitude breeding grounds (Steiner et al. 2012), where they often seem to appear in numbers rather than individually (personal observation and unpublished land based data observations in the Azores archipelago). This suggests that some animals may travel in groups when returning to breeding grounds. By potentially maintaining bonds acquired during early stages of dispersal, young males forming ‘bachelor’ groups composed of animals of the same age/size (Best 1979, Frantzi and Alexiadou 2008, Gaskin 1970, Ohsumi 1971), as were whale 1 and 35 in this study (known because these were acoustically measured in Miller et al. (2013b), where they were classified as whales NN20 and HL140), could benefit by improved success in returning to breeding grounds through cooperation (Nowak 2006). Coupled with benefits of group behaviour in protection against predators (Elgar 1989) and advantages in group foraging success (Beauchamp 2005), this may help to explain long-term bonds between males, particularly for animals that are not fully grown and may lack experience, as is the case of those found in Kaikoura (Miller et al. 2013b).

4.4.2. *Coda-creaks*

Coda-creaks found in this study matched sound properties, such as its duration and inter-click interval, with those reported by others (Gordon 1987, Paulos 2007, Weilgart 1990, Whitehead 2003), and sounded clearly distinct from feeding creaks (Weilgart 1990). The context here was, however, different. Most coda-creaks have been associated with the presence of codas during socializing periods where females and immatures are at or close to the surface (Weilgart 1990, Whitehead and Weilgart 1991). Here, coda-creaks were found in the middle of a foraging dive performed by two males during which codas and slow clicks were heard. While coda-creaks have been suggested to have a commutative and/or echolocation function during socializing periods (Gordon 1987, Weilgart 1990), Whitehead (2003) suggests, based on their ICI, that coda-creaks are suitable for brief sonar assessment of objects or group members at ranges between 30-80 m, in accordance with the estimated scanning distance of 37.5 m extracted from the average ICI of my coda-creaks. Although the feeding creaks heard just before and after coda-creaks could not be allocated to either whale, it is possible that the whale emitting coda-creaks was assessing the movements and orientation of the whale performing the creaks to gather information on prey location.

Future analysis of the spectrum frequency of coda-creaks, how this varies within the click train, as well as a detailed look at their waveform structure could bring new insights into its function.

4.4.3. *Stereotyped patterns of clicks*

4.4.3.1. *Slow click codas (SCcodas)*

The observation of repeated stereotyped patterns of clicks displaying spectral characteristics and waveform patterns similar to those of slow clicks, and different from CCodas (other codas), appears to be unique. In addition to the relative amplitude and centre frequency differences, the longer duration of SCcodas compared with that of CCodas and the presence of single slow clicks and bouts with short ICIs within sequences of SCcodas, supports the idea that SCcodas are a specific vocalisation type. SCcodas were only associated with the ascending phase of this one complete dive cycle performed by the pair of whales. Although based on a single observation and not representative of a population, it is worth noting that SCcodas, like slow click bouts (Jaquet et al. 2001, Oliveira et al. 2013), were only present during the ascending phase of a foraging dive.

It is not clear if previous studies on codas (Antunes et al. 2011, Marcoux et al. 2006, Rendell and Whitehead 2003a) looked at their spectral frequency and waveform in detail, as most studies have investigated coda temporal patterns (Pavan et al. 2000, Watkins and Schevill 1977, Weilgart and Whitehead 1993, 1997). For these reasons, and considering the thousands of codas analysed in most of these studies, it is possible that clicks matching those found here (SCcodas) were missed. Alternatively, since most coda studies have focussed on social units of females and immature offspring, SCcodas may represent a new click type only produced by males.

SCcodas showed different spectral frequencies to slow clicks. The SCcodas found here may not be intended to match slow click properties, but a different form of codas with lower frequency and higher relative amplitude. The centre frequency of regular clicks has been reported to be as low as 2 kHz (Goold and Jones 1995) and up to 32 kHz (Backus and Schevill 1966). While this could be due to poor reporting standards (Madsen et al. 2002b), it is possible that my SCcodas could be attributed to a variation of regular clicks, used with shorter ICIs. The different pulse decay rate between my CCodas and the codas recorded by Madsen and colleagues (2002a) and Whitehead (2003) can be explained by the directionality effects of

sperm whale clicks, where the whale orientation affects the waveform structure as perceived from the location of the hydrophone (Madsen et al. 2002a). Alternatively, physiological constraints may apply when using lower frequency clicks with such small inter-click intervals, as those found on SCcodas (mean = 0.31 s, SD=0.08).

The suggestion that individual whales need to alter the configuration of their sound apparatus in order to produce different click types (Madsen et al. 2002a), is consistent with previous observations that whales take 10 s to switch from coda producing mode into regular clicking mode (Madsen et al. 2002a), and with my observation, in which the time between the last CCoda (from a series of six with mean inter-coda interval of 5 s) and the first SCcoda was 18.4 s. My observations assume that the same whale produced both coda types, which is likely due to bearing measurements.

4.4.3.2. *Codas*

Codas, as repeated series of stereotyped clicks, could have been used by the pair of whales to identify their acoustic clan history, perhaps indicating the breeding grounds from which they originated (Weilgart and Whitehead 1997).

The most commonly detected coda type in this study, the 1+2, matches a coda type from the “short” clan, from Rendell and Whitehead (2003b), only used by one of 22 social units (unit T), studied in the Galápagos Archipelago, and was also detected in clan “++1/+1+1”, recorded off Tonga. The second most commonly detected coda, the 1+3 matched the “short” clan from the Galápagos, where it was recorded from nine different social units and from three additional units from the “4+” clan, reported to be present in all regions from the South Pacific (Rendell and Whitehead 2003b).

Coda 1+2+1 (n=1) which was the only exclusively SCcoda, matched one from Japan, as well as with eight social units from the “short” clan in the Galápagos, one social unit from clan “++1/+1+1” from Tonga, four units from the “4+” clan spread thorough the South Pacific, and two units from the “regular” clan in the Galápagos Islands (Rendell and Whitehead 2003b).

Codas composed of two clicks only, either have not been found previously (Amano et al. 2014) or have been excluded from analysis due to being rare and/or difficult to identify (Weilgart and Whitehead 1997). Frantzis and Alexiadou (2008) reported one of these codas and suggested it could have been an accidental, or intentional change of a three click coda since it preceded a coda of the same “[root]” family. Here the only two clicks coda found was the first of a sequence of three codas after a series of SCcodas (see Figure 4.1).

While definite conclusions cannot be drawn about the origins of the codas recorded, and hence the pair of whales 1 and 35, it is possible that these animals originated from a social unit from any of the matched locations, especially considering the large-scale moving patterns of males (Whitehead 2003). However most coda types matched those from breeding grounds within the same ocean basin, i.e., the Pacific Ocean, given my coda definition did not satisfy all coda classification criteria used in other studies, my match results may be inaccurate.

4.4.4. *Slow clicks*

The mode and context in which slow clicks were observed included repeated stereotyped patterns of clicks (like codas) lasting under a second, single clicks, and bouts of clicks with long ICIs between c. 4 and 7 s, at times overlapping with coda series. This observation challenges the hypothesis that slow clicks in high latitude male-only feeding grounds may be used for acoustic display in competition for food aggregations (Madsen et al. 2002b), but supports the hypothesis that slow clicks have a role in communication between males (Barlow and Taylor 2005, Gordon 1987, Madsen et al. 2002b, Mullins et al. 1988, Oliveira et al. 2013, Weilgart and Whitehead 1988, Whitehead 1993). That the pair of whales actively approached each other during two consecutive surfacings, while maintaining proximity and emitting codas during the submerged phase strongly suggests that the whales were not in competition mode but were displaying some kind of non-agonistic social behaviour.

If slow clicks were used as a form of communication, their meaning, like codas (Whitehead 2003), is unknown (Oliveira et al. 2013). The presence of slow clicks and codas during my observation, and that codas are used by female family units to identify members of their own acoustic clan and maintain and reinforce group cohesion (Rendell and Whitehead 2003b, Watkins and Schevill 1977), suggests that in this context, slow clicks and codas may each serve a different communication function. Additionally, the higher number of slow click events per dive found here compared with the average found for the prior ninety-four dives analysed, suggests the whales used more slow clicks than average, even though these results could not be compared statistically because current results included slow click counts from both whales whereas prior results were based on individual whales.

Frequency spectrum differences in vocalisations may be related to the size of the structures responsible for the sound production (Tyack and Clark 2000). Seven hundred Hz differences between centre frequencies of slow clicks produced by different males have been reported, although the sizes of the individuals involved were not known (Madsen et al. 2002b).

The use of codas observed here may allow whales to update each other on their foraging phase, as suggested for non-solitary males and females from the Mediterranean, where some coda types were linked to specific foraging dive phases (Frantzis and Alexiadou 2008), while slow clicks may communicate information related to the size of the whale, hence passing on potential individual identification features (Gordon 1987, Madsen et al. 2002b, Mullins et al. 1988, Whitehead 2003). However, as slow click patterns at male-only feeding grounds are mostly associated with bouts of clicks produced by ascending whales before surfacing (Jaquet et al. 2001, Oliveira et al. 2013) also reported in Chapter 2, it is likely that slow clicks also function to inform other whales of their foraging dive phase, as proposed for codas in the Mediterranean (Frantzis and Alexiadou 2008).

Because slow clicks are estimated to reach longer distances than both regular and creak clicks (60 km vs. 16 km and 6 km respectively (Madsen et al. 2002b)), my observation of a slow click bout from a distant whale during overlapping codas and slow clicks of the pair of whales being analysed, questions whether the slow clicks from the pair of whales were a reaction to the distant slow clicks rather than related to the nearby whale.

4.4.5. *Conclusions*

- My study shows that male sperm whales in a high latitudes male-only feeding ground may engage in social interactions, including body coordination and the use of communication clicks as codas and coda-creaks, while actively foraging.
- Stereotyped patterns of clicks with waveform and spectral characteristics significantly different from ‘traditional’ codas, revealed what seems to be a new click type used in time patterns similar to those found in codas, also distinguished by a higher relative amplitude and a longer duration compared with ‘traditional’ codas.
- The function of slow clicks within this context does not seem to be related to competition for foraging space and it could have been used for communication in conjunction with codas.

4.5. References

- Amano, M., A. Kourogi, K. Aoki, M. Yoshioka, and K. Mori. 2014. Differences in sperm whale codas between two waters off Japan: possible geographic separation of vocal clans. *Journal of Mammalogy* **95**(1):169-175.
- Antunes, R. 2009. Variation in sperm whale (*Physeter macrocephalus*) coda vocalizations and social structure in the North Atlantic Ocean. PhD thesis. University of St Andrews, St Andrews, Scotland.
- Antunes, R., T. Schulz, S. Gero, H. Whitehead, J. C. D. Gordon, and L. Rendell. 2011. Individually distinctive acoustic features in sperm whale codas. *Animal Behaviour* **81**(4):723-730.
- Backus, R. H., and W. E. Schevill. 1966. Physeter clicks. Pages 510–528 in K. S. Norris, editor. *Whales, dolphins, and porpoises*. University of California Press, Berkeley.
- Barlow, J., and B. L. Taylor. 2005. Estimates of sperm whale abundance in the northeastern temperate Pacific from a combined acoustic and visual survey. *Marine Mammal Science* **21**(3):429-445.
- Beauchamp, G. 2005. Does group foraging promote efficient exploitation of resources? *Oikos* **111**(2):403-407.
- Best, P. B. 1979. Social organization in sperm whales, *Physeter macrocephalus*. Pages 227-289 in H. E. Winn and B. L. Olla, editors. *Behavior of Marine Animals*. Springer US.
- Caldwell, D. K., M. C. Caldwell, and D. W. Rice. 1966. Behavior of the sperm whale *Physeter catodon* L. Pages 677–717 in K. S. Norris, editor. *Whales, dolphins and porpoises*. University of California Press, Berkeley.
- Charif, R. A., A. M. Waack, and L. M. Strickman. 2008. Raven Pro 1.3 User's Manual. The Cornell Laboratory of Ornithology, Ithaca, New York.
- Christal, J., and H. Whitehead. 1997. Aggregations of mature male sperm whales on the Galápagos Islands breeding ground. *Marine Mammal Science* **13**(1):59-69.
- David, L. 2002. Disturbance to Mediterranean cetaceans caused by vessel traffic. Report prepared for the ACCOBAMS Secretariat, Monaco.
- Dawson, S. M., E. Slooten, and O. Jake. 1994. Distribution, abundance and population structure of sperm whales at Kaikoura. WWF-NZ, Wellington.
- De Stephanis, R., J. Giménez, E. Carpinelli, C. Gutierrez-Exposito, and A. Cañadas. 2013. As main meal for sperm whales: plastics debris. *Marine Pollution Bulletin* **69**(1-2):206-214.
- Drouot-Dulau, V., and A. Gannier. 2007. Movements of sperm whale in the western Mediterranean Sea: preliminary photo-identification results. *Journal of the Marine Biological Association of the UK* **87**(1):195-200.
- Drouot, V., M. Bérubé, A. Gannier, J. C. Goold, R. J. Reid, and P. J. Palsboll. 2004a. A note on genetic isolation of Mediterranean sperm whales (*Physeter macrocephalus*) suggested by mitochondrial DNA. *Journal of Cetacean Research and Management* **6**(1):29-32.
- Drouot, V., J. C. Goold, and A. Gannier. 2004b. Regional diversity in the social vocalizations of sperm whale in the Mediterranean Sea. *La terre et la vie - Revue d'Ecologie* **59**:545-558.

- Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews* **64**(1):13-33.
- Engelhaupt, D., A. R. Hoelzel, C. Nicholson, A. Frantzis, S. Mesnick, S. Gero, H. Whitehead, L. Rendell, P. J. O. Miller, and R. De Stefanis. 2009. Female philopatry in coastal basins and male dispersion across the North Atlantic in a highly mobile marine species, the sperm whale (*Physeter macrocephalus*). *Molecular Ecology* **18**(20):4193-4205.
- Frantzis, A., and P. Alexiadou. 2008. Male sperm whale (*Physeter macrocephalus*) coda production and coda-type usage depend on the presence of conspecifics and the behavioural context. *Canadian Journal of Zoology* **86**(1):62-75.
- Gaskin, D. E. 1970. Composition of schools of sperm whales *Physeter catodon* Linn. east of New Zealand. *New Zealand Journal of Marine and Freshwater Research* **4**(4):456-471.
- Gaskin, D. E., and M. W. Cawthorn. 1967. Diet and feeding habits of the sperm whale (*Physeter catodon* L.) in the Cook Strait region of New Zealand. *New Zealand Journal of Marine and Freshwater Research* **1**(2):156-179.
- Gero, S., D. Engelhaupt, L. Rendell, and H. Whitehead. 2009. Who cares? Between-group variation in alloparental caregiving in sperm whales. *Behavioral Ecology* **20**(4):838-843.
- Gero, S., J. C. D. Gordon, and H. Whitehead. 2015. Individualized social preferences and long-term social fidelity between social units of sperm whales. *Animal Behaviour* **102**:15-23.
- Gero, S., M. Milligan, C. Rinaldi, P. Francis, J. Gordon, C. Carlson, A. Steffen, P. Tyack, P. Evans, and H. Whitehead. 2014. Behavior and social structure of the sperm whales of Dominica, West Indies. *Marine Mammal Science* **30**(3):905-922.
- Gillespie, D. 1997. An acoustic survey for sperm whales in the Southern Ocean Sanctuary conducted from the RSV Aurora Borealis. *Reports of the International Whaling Commission* **47**:897-907.
- Gillespie, D., D. K. Mellinger, J. C. D. Gordon, D. McLaren, P. Redmond, R. McHugh, P. W. Trinder, X. Y. Deng, and A. Thode. 2009. PAMGUARD: Semiautomated, open source software for real-time acoustic detection and localisation of cetaceans. *Journal of the Acoustical Society of America* **125**(4):2547.
- Goold, J. C., and S. E. Jones. 1995. Time and frequency domain characteristics of sperm whale clicks. *Journal of the Acoustical Society of America* **98**(3):1279-1291.
- Gordon, J. C. D. 1987. Sperm whale groups and social behaviour observed off Sri Lanka. PhD thesis. University of Cambridge, Cambridge, England.
- Gordon, J. C. D., R. Leaper, F. G. Hartley, and O. Chappell. 1992. Effects of whale-watching vessels on the surface and underwater acoustic behaviour of sperm whales off Kaikoura, New Zealand. Department of Conservation. Science & Research Series No. 52, 35 pp.
- Gordon, J. C. D., and L. Steiner. 1992. Ventilation and dive patterns in sperm whales, *Physeter macrocephalus*, in the Azores. *Reports of the International Whaling Commission* **42**:561-565.
- Ivashin, M. V. 1967. Whale globe-trotter. *Priroda* (Moscow) **8**:105-107.
- Jaquet, N., S. Dawson, and L. Douglas. 2001. Vocal behaviour of male sperm whales: why do they click? *Journal of the Acoustical Society of America* **109**(5):2254-2259.

- Jaquet, N., S. Dawson, and E. Slooten. 2000. Seasonal distribution and diving behaviour of male sperm whales off Kaikoura: foraging implications. *Canadian Journal of Zoology* **78**(3):407-419.
- Lettevall, E., C. Richter, N. Jaquet, E. Slooten, S. Dawson, H. Whitehead, J. Christal, and P. M. Howard. 2002. Social structure and residency in aggregations of male sperm whales. *Canadian Journal of Zoology* **80**(7):1189-1196.
- Lyrholm, T., and U. Gyllenstein. 1998. Global matrilineal population structure in sperm whales as indicated by mitochondrial DNA sequences. *Proceedings of the Royal Society of London B: Biological Sciences* **265**(1406):1679-1684.
- Madsen, P. T., R. Payne, N. U. Kristiansen, M. Wahlberg, I. Kerr, and B. Møhl. 2002a. Sperm whale sound production studied with ultrasound time/depth-recording tags. *Journal of Experimental Biology* **205**(Pt13):1899-1906.
- Madsen, P. T., M. Wahlberg, and B. Møhl. 2002b. Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and communication. *Behavioral Ecology and Sociobiology* **53**(1):31-41.
- Marcoux, M., H. Whitehead, and L. Rendell. 2006. Coda vocalizations recorded in breeding areas are almost entirely produced by mature female sperm whales (*Physeter macrocephalus*). *Canadian Journal of Zoology* **84**(4):609-614.
- Markowitz, T. M., C. F. Richter, and J. C. D. Gordon. 2011. Effects of tourism on the behaviour of sperm whales inhabiting the Kaikoura Canyon. Report submitted to the New Zealand Department of Conservation by PACE-NZRP, Kaikoura Sperm Whale and Tourism Research Project, 20 December 2011, 121 pp.
- Mendes, S., N. Jason, R. J. Reid, A. F. Zuur, and G. J. Pierce. 2007. Stable carbon and nitrogen isotope ratio profiling of sperm whale teeth reveals ontogenetic movements and trophic ecology. *Oecologia* **151**(4):605-615.
- Mesnick, S. L. 2001. Genetic relatedness in sperm whales: evidence and cultural implications. *Behavioral and brain sciences* **24**(2):346-347.
- Miller, B. S. 2010. Acoustically derived growth rates and three-dimensional localisation of sperm whales (*Physeter macrocephalus*) in Kaikoura, New Zealand. PhD thesis. University of Otago, Dunedin, New Zealand.
- Miller, B. S., S. Dawson, and R. Vennell. 2013a. Underwater behavior of sperm whales off Kaikoura, New Zealand, as revealed by a three-dimensional hydrophone array. *Journal of the Acoustical Society of America* **134**(4):2690-2700.
- Miller, B. S., A. Growcott, E. Slooten, and S. M. Dawson. 2013b. Acoustically derived growth rates of sperm whales (*Physeter macrocephalus*) in Kaikoura, New Zealand. *Journal of the Acoustical Society of America* **134**(3):2438-2445.
- Miller, P. J. O., M. P. Johnson, and P. L. Tyack. 2004. Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. *Proceedings of the Royal Society of London B: Biological Sciences* **271**(1554):2239-2247.
- Moore, K. E., W. A. Watkins, and P. L. Tyack. 1993. Pattern similarity in shared codas from sperm whales (*Physeter catodon*). *Marine Mammal Science* **9**(1):1-9.

- Mullins, J., H. Whitehead, and L. S. Weilgart. 1988. Behaviour and vocalizations of two single sperm whales, *Physeter macrocephalus*, off Nova Scotia. Canadian Journal of Fisheries and Aquatic Sciences **45**(10):1736-1743.
- Norris, K. S. 1966. Whales, dolphins, and porpoises. University of California Press, Berkeley.
- Nowak, M. A. 2006. Five rules for the evolution of cooperation. Science **314**(5805):1560-1563.
- Ohsumi, S. 1971. Some investigations on the school structure of sperm whale. Tokyo 23 (1971): 1-25.
- Oliveira, C., M. Wahlberg, M. Johnson, P. J. O. Miller, and P. T. Madsen. 2013. The function of male sperm whale slow clicks in a high latitude habitat: communication, echolocation, or prey debilitation? Journal of the Acoustical Society of America **133**(5):3135-3144.
- Paulos, R. L. D. 2007. Sperm whale (*Physeter macrocephalus*) codas and creaks in the Northern Gulf of Mexico: classification, comparison, and co-occurrence. University of Southern Mississippi, Hattiesburg, USA.
- Pavan, G., T. J. Hayward, J. F. Borsani, M. Priano, M. Manghi, C. Fossati, and J. C. D. Gordon. 2000. Time patterns of sperm whale codas recorded in the Mediterranean Sea 1985-1996. Journal of the Acoustical Society of America **107**(6):3487-3495.
- Pinela, A. M., S. Qu  rouil, S. Magalh  es, M. A. Silva, R. Prieto, J. A. Matos, and R. S. Santos. 2009. Population genetics and social organization of the sperm whale (*Physeter macrocephalus*) in the Azores inferred by microsatellite analyses. Canadian Journal of Zoology **87**(9):802-813.
- Rendell, L. E., and H. Whitehead. 2003a. Comparing repertoires of sperm whale codas: a multiple methods approach. Bioacoustics **14**(1):61-81.
- Rendell, L. E., and H. Whitehead. 2003b. Vocal clans in sperm whales (*Physeter macrocephalus*). Proceedings of the Royal Society of London B: Biological Sciences **270**(1512):225-231.
- Rice, D. W. 1989. Sperm whale, *Physeter macrocephalus* (Linnaeus, 1758). Pages 177-233 in S. H. Ridgway and R. Harrison, editors. Handbook of Marine Mammals. Academic Press, London, UK.
- Richter, C., S. Dawson, and E. Slooten 2006. Impacts of commercial whale watching on male sperm whales at Kaikoura, New Zealand. Marine Mammal Science **22**(1):46-63.
- Richter, C. F., S. Dawson, and E. Slooten. 2003. Sperm whale watching off Kaikoura, New Zealand: effects of current activities on surfacing and vocalisation patterns. Science for Conservation Series No. 219. Department of Conservation, Wellington.
- Roberts, S. M. 2003. Examination of the stomach contents from a Mediterranean sperm whale found south of Crete, Greece. Journal of the Marine Biological Association of the UK **83**(3):667-670.
- Schulz, T. M., H. Whitehead, S. Gero, and L. Rendell. 2011. Individual vocal production in a sperm whale (*Physeter macrocephalus*) social unit. Marine Mammal Science **27**(1):149-166.
- Steiner, L., L. U. Lamoni, M. A. Plata, S. K. Jensen, E. Lettevall, and J. C. D. Gordon. 2012. A link between male sperm whales, *Physeter macrocephalus*, of the Azores and Norway. Journal of the Marine Biological Association of the UK **92**(8):1751-1756.

- Teloni, V., M. P. Johnson, P. J. O. Miller, and P. T. Madsen. 2008. Shallow food for deep divers: dynamic foraging behavior of male sperm whales in a high latitude habitat. *Journal of Experimental Marine Biology and Ecology* **354**(1):119-131.
- Tyack, P. L., and C. W. Clark. 2000. Communication and acoustic behavior of dolphins and whales. Pages 156-224 in W. W. L. Au, A. N. Popper, and R. R. Fay, editors. *Hearing by whales and dolphins*. Springer -Verlag, New York, 485 pp.
- Van der Linde, M. 2010. Long-term monitoring of sperm whales in Kaikoura, New Zealand: data-management, abundance, and population dynamics. MSc thesis. University of Otago, Dunedin, New Zealand.
- Watkins, W. A., K. E. Moore, and P. L. Tyack. 1985. Sperm whale acoustic behaviors in the southeast Caribbean. *Cetology* **49**:1-15.
- Watkins, W. A., and W. E. Schevill. 1977. Sperm whale codas. *Journal of the Acoustical Society of America* **62**(6):1485-1490.
- Watwood, S. I., P. J. O. Miller, M. P. Johnson, P. T. Madsen, and P. L. Tyack. 2006. Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *Journal of Animal Ecology* **75**(3):814-825.
- Weilgart, L., and H. Whitehead. 1993. Coda communication by sperm whales (*Physeter macrocephalus*) off the Galápagos Islands. *Canadian Journal of Zoology* **71**(4):744-752.
- Weilgart, L., and H. Whitehead. 1997. Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behavioral Ecology and Sociobiology* **40**(5):277-285.
- Weilgart, L. S. 1990. Vocalizations of the sperm whale (*Physeter macrocephalus*) off the Galápagos Islands as related to behavioral and circumstantial variables. PhD thesis. Dalhousie University, Halifax, Nova Scotia.
- Weilgart, L. S., and H. Whitehead. 1988. Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). *Canadian Journal of Zoology* **66**(9):1931-1937.
- Whitehead, H. 1987. Social organization of sperm whales off the Galápagos: implications for management and conservation. *Reports of the International Whaling Commission* **37**:195-199.
- Whitehead, H. 1993. The behaviour of mature male sperm whales on the Galápagos Islands breeding grounds. *Canadian Journal of Zoology* **71**(4):689-699.
- Whitehead, H. 2003. *Sperm whales: social evolution in the ocean*. University of Chicago Press 413 pp.
- Whitehead, H., V. Papastavrou, and S. C. Smith. 1989. Feeding success of sperm whales and sea-surface temperature off the Galápagos Islands. *Marine Ecology Progress Series* **53**(2):201-203.
- Whitehead, H., S. Waters, and T. Lyrholm. 1991. Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. *Behavioral Ecology and Sociobiology* **29**(5):385-389.
- Whitehead, H., and L. Weilgart. 1990. Click rates from sperm whales. *Journal of the Acoustical Society of America* **87**(4):1798-1806.
- Whitehead, H., and L. Weilgart. 1991. Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. *Behaviour* **118**(3-4):275-296.

5. Relationship of bathymetry and commercial fisheries with sperm whale creaks

Abstract

Sperm whales (*Physeter macrocephalus*) use a rapid series of clicks (called creaks or buzzes), with short duration and high directionality during their final approach to prey. These may be up to 90 clicks per second, and creaks may last from a few seconds to several minutes. Creaks have been used to gather information about foraging behaviour, prey type, and to estimate average prey size based on creak rates and daily food requirements. Sperm whales are opportunistic top predators that feed primarily on mesopelagic cephalopods during long and deep dives. Males diversify their diet with age and during dispersal towards higher latitudes, where fish become a significant part of their diet. Using passive acoustic monitoring, 95 complete dives from 14 males from the Kaikoura canyon were analysed in terms of creak rates and duration, which were correlated with bathymetric features and sites of local fisheries targeting species known to be consumed by sperm whales in the region. On average, whales produced 7.8 creaks per dive and mean creak duration was high, at 27.1 s (N=741), with the longest creak lasting 5.6 min. Bottom slope, depth and proximity to commercial fisheries was significantly correlated with sperm whale locations when producing creaks. Compared with other study areas around the world, the long creaks found off Kaikoura suggest that whales in this area may follow a foraging strategy based on fewer but larger and/or more nutritious prey compared to other areas.

5.1. Introduction

Sperm whales (*Physeter macrocephalus*) are apex predators that are found throughout the world's deep oceans (Rice 1989). Different sexes, however, have different body sizes, geographical distribution, social habits, foraging strategies and diets (Best 1979, Best 1999, Gaskin and Cawthorn 1967, Lettevall et al. 2002, Rice 1989, Teloni et al. 2008). Females and immature offspring live in social long-term family units, predominantly between 40° N and 40° S, where they mostly feed on mesopelagic-bathypelagic cephalopods (Clarke 1996, Whitehead 2003). In order to reach physical maturity and become competitive when returning to breeding grounds, males need to grow about 1/3 longer and 2/3 heavier than females (Best 1979, Whitehead 1994). This is thought to be the primary cause for the sexual segregation of this species, where males disperse to higher latitudes in search for richer and more diverse feeding grounds (Teloni et al. 2008). During dispersal, fish can become a significant part of the males' diet (Clarke 1996, Clarke et al. 1993, Gaskin and Cawthorn 1967, Martin and Clarke 1986). Worldwide, sperm whale stomach contents have revealed c. 56 species of cephalopods from 24 families and over 68 species of fish from 49 families (Clarke 1996, Kawakami 1980), making the sperm whale an opportunistic predator that seems to explore the most abundant cephalopod or fish species present in their foraging area (Clarke 1980). The fish species consumed by male sperm whales in the Cook Strait region, for example, vary both from month to month and consistently across different animals (Gaskin and Cawthorn 1967).

Foraging sperm whales use 'regular clicks': a long range directional bio-sonar, known as echolocation, which potentially enables detection of prey resources at distances up to 1000 m (Madsen et al. 2007, Møhl et al. 2003). These clicks occur at intervals between 0.5-2 s (Jaquet et al. 2001) and their inter-click intervals (ICIs) are an indicator of the maximum inspection range (Fais et al. 2015). The rate at which clicks are produced increases drastically, up to about 90 clicks/second (Jaquet et al. 2001), when whales home in on their prey. These fast repetition clicks, called 'creaks' by Gordon (1987), are recognised as feeding attempts during which the whales significantly increase manoeuvring of their body orientation (Miller et al. 2004a), comparable to the terminal echolocation buzz produced by bats while foraging on insects (Griffin et al. 1960).

Compared with regular clicks, creak clicks have lower apparent source levels (ASL) and shorter durations, while still showing high directionality (Madsen et al. 2002b). Creaks are generally preceded by a train of regular clicks and can be identified by a doubling of repetition rates in the ICIs of two consecutive regular clicks (Fais et al. 2015). Creaks are often followed

by a silent period lasting several seconds, thought to represent the time during which the whale is ingesting its prey (Whitehead 2003). Usually, creaks last up to 40 s (Gordon 1987, Madsen et al. 2002b, Miller et al. 2004a, Mullins et al. 1988, Teloni et al. 2008, Whitehead 2003, Whitehead and Weilgart 1990, Whitehead and Weilgart 1991), however, a few creaks longer than 70 s (Teloni et al. 2008) and 130 s (Mullins et al. 1988) have been recorded from males.

Sperm whale prey have been identified using stomach content analysis (Clarke 1996, Clarke and Pascoe 1997, Judkins et al. 2015), faecal sample analysis (Gordon 1987, Smith and Whitehead 2000) or, more recently, stable isotope analysis (Mendes et al. 2007). However, neither the prey type, nor prey capture rate associated with creaks is known (Teloni et al. 2008). Also unknown is whether sperm whales take prey without producing sound or, indeed, if multiple prey can be taken with a single creak. In echolocating bats, the presence of a buzz reflects an attempt to catch a single prey, where longer buzzes are associated with longer chases (Griffin et al. 1960, Kalko 1995).

The time between creaks and the duration of creaks produced by males has been associated with the whale's depth, where shallower dives tend to be associated with longer creaks spaced further apart than for deep dives, suggesting a pattern where sperm whales forage on denser patches of smaller prey at depth, and on widely distributed prey (presumably fish) that require a longer active chase during shallow dives (Fais et al. 2015, Miller et al. 2013a, Teloni et al. 2008). As males are significantly larger than females, one would expect either higher prey consumption of similar prey to that targeted by females, or the consumption of either larger, or more nutritional, prey. The difficulty of observing interactions between sperm whales and their prey results in a lack of knowledge regarding the prey type and size consumed and its relationship with creak characteristics, as well as how these variables relate with prey habitat preferences.

Off the male feeding ground near Kaikoura (Childerhouse et al. 1995, Douglas et al. 2005, Sagnol et al. 2014, Van der Linde 2010), whales show different spatial distribution and diving behaviour between summer and winter months. These differences are thought to be related to fluctuations in availability of prey (Jaquet et al. 2000), such as groper, or hāpuku (*Polyprion oxygeneios*), an important seasonal commercial and recreational fishery in the region (Paul 2002). Gaskin and Cawthorn (1967) found several commercially fished species in the stomach contents of males captured in this region, including groper, ling, kingfish, conger eel, and dory species. Additionally, sperm whales from Kaikoura are recurrently seen preying on fast moving fish at the surface (Miller et al. 2013a).

I used visual and acoustic data to quantify creak rates and creak duration from 95 complete dive cycles from 14 individually identified male sperm whales foraging in the Kaikoura canyon. This information was then analysed with regards to the slope and depth of the habitat and the proximity to known commercial local fishing activities targeting fish species known as sperm whale prey in this region.

5.2. Methods

5.2.1. Field work

Acoustical and visual data were collected between October 2009 and June 2011 in the Kaikoura canyon, south of the Kaikoura peninsula, on the East coast of South island of New Zealand (Figure 2.1; Chapter 2).

Data collection and filtering, selection of data for analysis, as well as animal identification and technical details of the acoustic hardware and software, were as described in detail in sections 2.2.1 - 2.2.3, in Chapter 2. A complete dive cycle (hereafter dive) was defined as the time between two consecutive fluke-up events (start of dive) from the same animal (Figure 2.2; Chapter 2).

5.2.2. Creak characteristics

Creaks were defined as high-repetition rate click series with inter-click intervals ≤ 0.1 s, following a similar definition (< 0.1 s) used by Whitehead and Weilgart (1990) and Weilgart (1990). This criteria roughly reflects the time when the ICIs stabilise after a rapid decrease during transition from regular to creak clicks (Jaquet et al. 2001). Due to its inherent characteristics of high directionality, lower ASL and shorter duration, creak clicks are sometimes difficult to detect from towed hydrophone recordings (Teloni 2005) and may not be detected by the click detector filtering process. For this reason, creak duration was defined as the time interval between the last regular click before a creak and the first regular click after a creak (Figure 5.1). As the ICIs change rapidly at the start and end of creaks, this is not likely to significantly affect the timing of the start and end of creaks (Fais et al. 2015). However, as sperm whales can be silent for up to 10 s after each creak (Gordon 1987, Jaquet et al. 2001) before resuming regular searching clicks, this method may result in an overestimation of the duration of creaks. Therefore, two additional creak duration parameters were defined: 1. *Creak detected mean*, defined as the mean time between the last regular click before the creak and the last detected creak click, and 2. *Creak detected max*, defined as the longest recorded time between the last regular click before the creak and the last creak click detected within every dive.

Only trains of at least two consecutive creak clicks (not echoes) were labelled within any creak click train. Creak clicks were distinguished from their echoes by inspection of their

bearings and waveforms. Bearings from creak clicks are consistently different from those of their echoes, showing a sharper waveform when compared with their nearest echo click. In order to guarantee that two creak clicks were consecutive, I lowered the playback speed of the sound file and matched the visual display of individual creak clicks with the audio playback, ensuring the presence of an echo click between every labelled creak click. The click detector filter frequently missed creak clicks (see example in Figure 5.1), although their presence was either confirmed through audio inspection (thus the creak was considered as continuing) or, after audio inspection failing to find creak clicks, the creak was considered to have ended when the filter picked up regular clicks. However, as regular click trains are interspaced with short silent periods (Gordon 1987, Madsen et al. 2002b, Miller et al. 2004b), it is possible that some creaks may have been wrongly identified as silences if the signal-to-noise ratio impeded automated detection during ‘silent’ periods and these were not heard during audio inspection. This may have underestimated the total number of creaks. Silences between bouts of regular clicks were defined as ICIs from regular clicks that were > 3 s and < 30 s, and where no creak clicks were detected or heard after manually listening to the recordings.

The method used to resolve uncertainty regarding the identity of regular clicks from the focal whale when these overlapped in bearing with those from other whales, or after silences preceded by an overlap, was described in detail in section 2.2.5 (Chapter 2). The same method was applied to find regular clicks from the focal whale following creaks that did not consistently show up on the click detector.

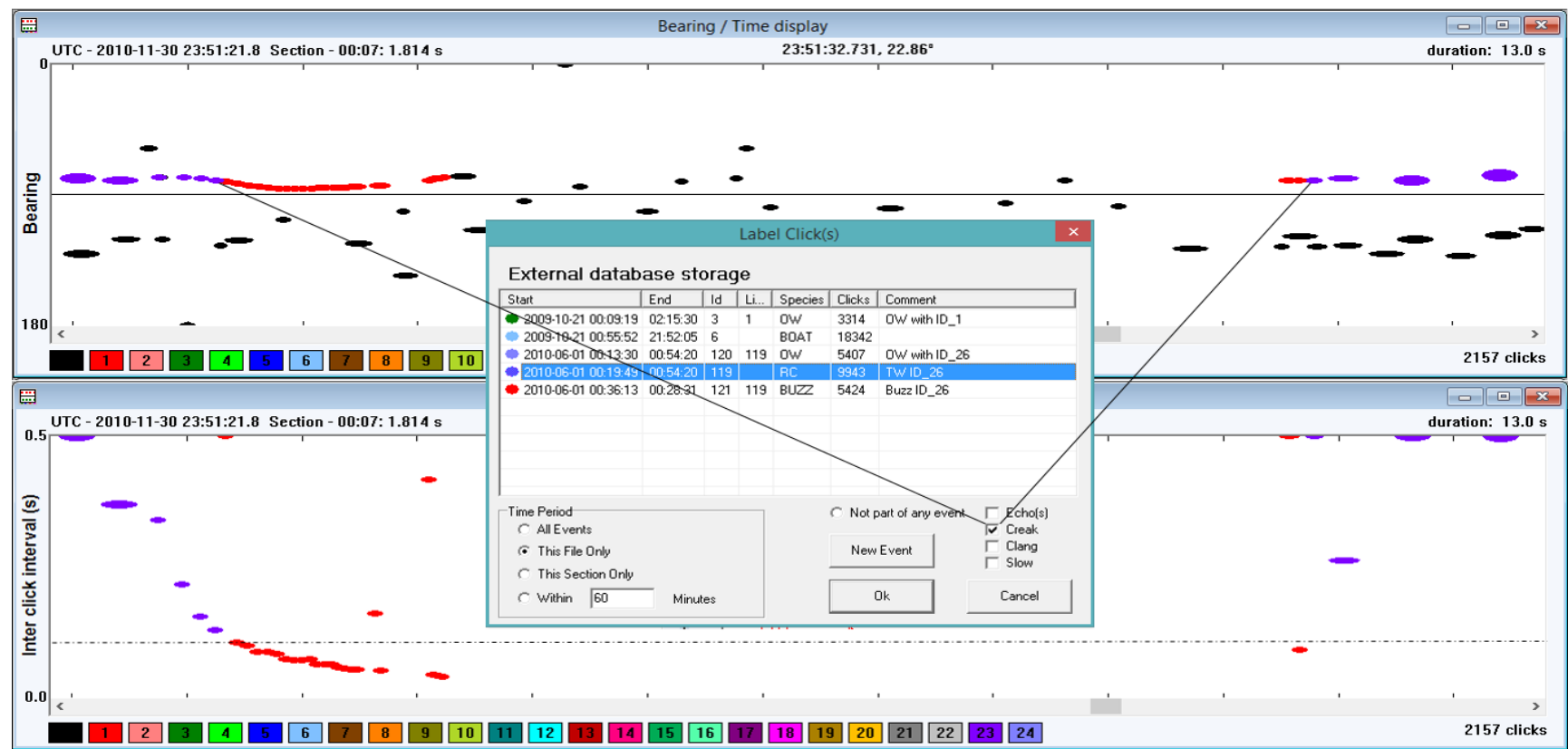


Figure 5.1 – Example of creak marking using the acoustic tracking software Rainbowclick. Main windows show the same sound file section (x-axis shows time over 13 s) where the top window shows click bearing (y-axis; zero bearing corresponds to a source directly in front of the vessel), and the lower window depicts inter-click interval (ICI) in s on the y-axis. Dashed line shows ICI threshold (≤ 0.1 s), defining a creak (see text). Regular clicks are highlighted in purple and creak clicks in red; note that, creak clicks missed by the filter, although present, result in apparent longer ICIs. Central window shows labelling of the last regular click before a creak and the first regular click after the creak used to calculate the duration of creaks.

5.2.3. *Habitat features associated with creaks*

I compared mean values of bottom slope and depth in order to determine how these parameters varied within the study area, defined as a rectangle encompassing all whale observations, and the whales' midpoint locations for each dive, including those without creaks, with creaks and with multiple creaks (for dives with 1 to 5 creaks in contrast to those with >5 creaks).

Bathymetry data were provided by the New Zealand National Institute of Water and Atmospheric Research (NIWA). ArcMap 10.1 (ESRI Spatial Analyst) was used for spatial analysis, including obtaining depth and slope data from the study area, as well as the midpoints of the whale's dives. Midpoints were used to standardise creak location (or their absence) within each dive, and were determined from the imaginary line joining the start and end of dives. This method resulted from an inability to get more precise information with this methodology (Miller 2010, Miller et al. 2013a). While the time and location of start and end of dives, as well as the exact time of creaks were known, the alternative method of estimating creak location based on time intervals and average swimming speeds along the track line separating diving and surfacing locations assumes that whales follow a straight line between consecutive surfacings, known to be incorrect for whales studied off Kaikoura (Miller et al. 2013a). The scale of the observation area (14.9 km x 32.7 km) in relation to the average horizontal distance travelled by the whales between the start and end of dives in this study (1958 m) and the fact that sperm whales do not creak while moving towards and from their chosen target depths (Jaquet et al. 2001, Miller et al. 2013a, Teloni et al. 2008), suggests that using midpoints may be an effective proxy for location.

5.2.4. *Fisheries data and relationship to creaks*

The aim of this analysis was to find whether the whales' estimated creak locations (dive midpoints with creak presence) were spatially associated with areas of local commercial fishing activities targeting species consumed by sperm whales. I ran two different analyses to account for the difference between the estimated catches of all fish, including sharks, and also estimated catches of only bony fish (groper and ling), under the assumption that these are the sperm whales' preferred target in the region (Gaskin and Cawthorn 1967).

Fisheries data were made available by the New Zealand Ministry of Primary Industries, MPI (Deed no. CAN2015-001). Data provided included estimated catch from commercial fisheries for the area encompassing all whale observations during the period in which field

work was conducted and catch estimates for species known to be consumed by male sperm whales in the region. Fishing methods included bottom and surface long-lining, trawling, set-nets, drift-nets and pair-set netting. Every fishing event had an associated date, species code, GPS location, fishing method and an estimated green weight (unprocessed) of the fish captured during the event. Unfortunately, spatial resolution of these data was hampered by GPS location being truncated rather than rounded and did not include accuracy to the nearest 0.1 min of latitude, resulting in clustered data. This limited my analyses and may have influenced the precision of the results.

Rectangular grid-cells were overlaid on the bathymetric image of the area covering all midpoint observations. Only those cells inside the red rectangle were used for analysis (see Figure 5.4 and Figure 5.5). The position, size and number of cells was set to maximise the chances of obtaining observations from both fisheries and whale midpoints within a cell, and to minimise the number of cells containing zero observations. Analysis consisted of counting the number of fishing events, or fishing event locations (several events may share the same location), and the number of midpoints, as well as the number of associated creaks for every grid cell to assess whether fishing-midpoint pair counts were associated within cells.

5.2.5. *Statistical analysis*

Data normality was assessed using Shapiro-Wilk tests (Shapiro and Wilk 1965). Where normal, data were analysed using unpaired t-tests; otherwise Mann-Whitney tests (Kasuya 2001) were used. Similarly, the strength and direction of association between the number of fishing observations and/or fishing locations, and midpoint dive locations or their number of associated creaks between adjacent equal-sized grid-cells, was tested using Pearson's correlations and Spearman's correlations.

A Kruskal–Wallis test was used to compare the duration of creaks between seasons using the median creak duration per dive per individual by season to account for independence between individuals. The same analysis was done using one dive per individual. Kruskal–Wallis tests were also used to compare the duration of creaks between individuals with four or more complete dives each. R (R Development Core Team 2015) software was used for all analyses.

5.3. Results

5.3.1. Creak characteristics

A total of 741 creaks were identified from 78 h of acoustic tracking of 14 male sperm whales, across 95 complete dive cycles. For all whales and for all dives, the average number of creaks per dive including dives without creaks (N=95) was 7.8 (SD=7.9; range 0-50), and their mean duration (only for dives with creaks, N=89) was 27.1 s (SD=17.3; range of means per dive 7.2-277.7 s). The creak detected mean (mean duration between the last regular click before a creak and the last detected creak click) was 15.7 s (SD=7.9; range of means per dive 0.09-210, N=741) and the mean for the longest creak per dive (creak detected max) was 50.5 s (SD=53.2; range of means per dive 0.09–338 s, N=741) (Table 5.1). On average, the whales went silent 15 times per dive (mean duration 10.1 s, SD=1.7, N=1420).

Between individuals no differences in creak duration was found ($n=81$, $H=8.85$, $Df=7$, $p=0.264$). Mean creak duration (per dive, per individual) did not vary by season ($H=1.52$, $Df=3$, $p=0.677$, $N=18$).

Eleven very long creaks > 100 s were found, including one of up 5.6 min (336 s). Although these were not analysed in detail, their occurrence seemed associated with proximity to the surface, either through the very clear creaks recorded and/or by visually spotting the animals at or near the surface. On three of these occasions, surface feeding (Miller et al. 2013a) occurred and the prey type was visually confirmed to be a fish. Confirmation twice occurred by overhead helicopters in radio contact with the research vessel, and once where an unidentified fish of c. 3 kg used the research vessel as a refuge, while the chasing whale kept swimming around the vessel on its side before abandoning its chase. The ICIs during long series of fast clicking, associated with surface feeding, often oscillated above and below the creak definition threshold, up to about 0.25 s, for short periods. This resulted in several creaks being labelled in what appeared to be a single chase.

Table 5.1 – Summary of creak rate and duration (s) per individual whale and per dive cycle.

Whale ID	N dives	N creaks	N creaks per dive (SD)	Mean creak duration (SD)	Creak detected mean (SD)	Creak detected max (SD)
1	44	299	6.8 (6.7)	34.3 (47.5)	19.6 (SD=37.9)	55.4 (63.9)
2	9	89	9.9 (5.3)	29.2 (6.5)	31.4 (SD=20.8)	79.1 (61.8)
3	4	14	3.5 (3)	28.4 (12.1)	17.2 (SD=14.9)	45.3 (64)
5	2	18	9 (1.4)	27.4 (2.3)	29.3 (SD=6.8)	76.7 (13.2)
6	3	72	24 (22.7)	16.8 (9)	14.6 (SD=8.3)	57.7 (15.2)
15	5	69	13.8 (4.9)	25.8 (4.8)	19.8 (SD=16.9)	65.9 (29.6)
18	2	17	8.5 (10.6)	9.5 (2.9)	5.4 (SD=1.9)	6.6 (5.3)
21	1	4	4	16.2	7.6	10.9
22	3	18	6 (5.3)	82.1 (64.6)	9.6 (SD=2.8)	30.1 (24.2)
25	6	16	2.7 (2.7)	30.3 (39.4)	14.3 (SD=5)	24.4 (8.8)
26	4	50	12.5 (12)	19.4 (4.5)	19.8 (SD=3.2)	41.3 (25.7)
27	4	19	4.8 (1.9)	21.8 (7.2)	12.7 (SD=3.9)	21.1 (4.3)
29	5	43	8.6 (9.1)	14.7 (30.4)	6.4 (SD=3.6)	18.3 (14.4)
36	3	13	4.3 (4.5)	23.5 (3.7)	12.3 (SD=1.5)	28.9 (15.7)
Total mean	-	-	7.8 (7.9)	27.1 (17.3)	15.7 (SD= 7.9)	50.5 (53.2)
Total	95	741	-	-	-	-

5.3.2. *Habitat features associated with creaks*

The average slope within the study area was significantly lower than that of whale's dive midpoints ($W=68118$, $Df=1978$, $p<0.002$; Figure 5.2), including those with creak presence ($W=59190$, $Df=1972$, $p<0.002$; Figure 5.2). Steeper slope angles were associated with dives with creaks compared to those without creaks ($W=73$, $Df=93$, $p=0.003$; Figure 5.2). However, slope did not vary between midpoints containing creaks, regardless of their number (1-5 and > 5 creaks per dive; $W=1130$, $Df=95$, $p=0.881$). Nevertheless, the average slope within the study area was significantly higher than that of midpoints of dives without creaks ($W=8929$, $Df=1889$, $p=0.014$; Figure 5.2).

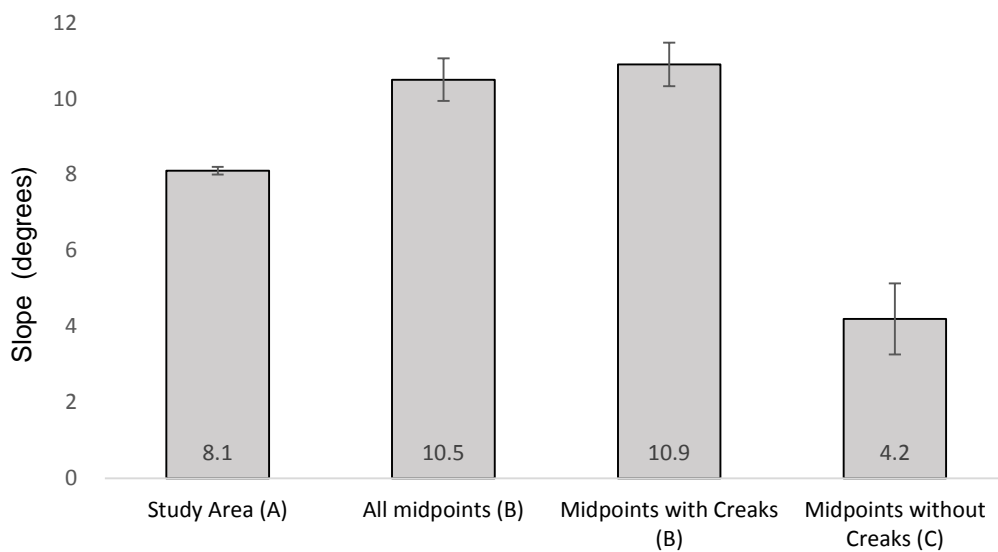


Figure 5.2 – Mean slope values (degrees) for the study area and dive midpoint observations; including dives with and without creak presence. Capital letters depict significant differences.

Midpoints of dives with creaks were associated with shallower waters than the average for the study area ($W=57600$, $Df=1569$, $p=0.046$) and for dives without creaks ($t=2.5009$, $Df=6$, $p=0.047$). Additionally, midpoints without creaks were associated with greater depths than all midpoints combined ($t=-2.3473$, $Df=5.956$, $p=0.058$). Other differences were not significant (Figure 5.3).

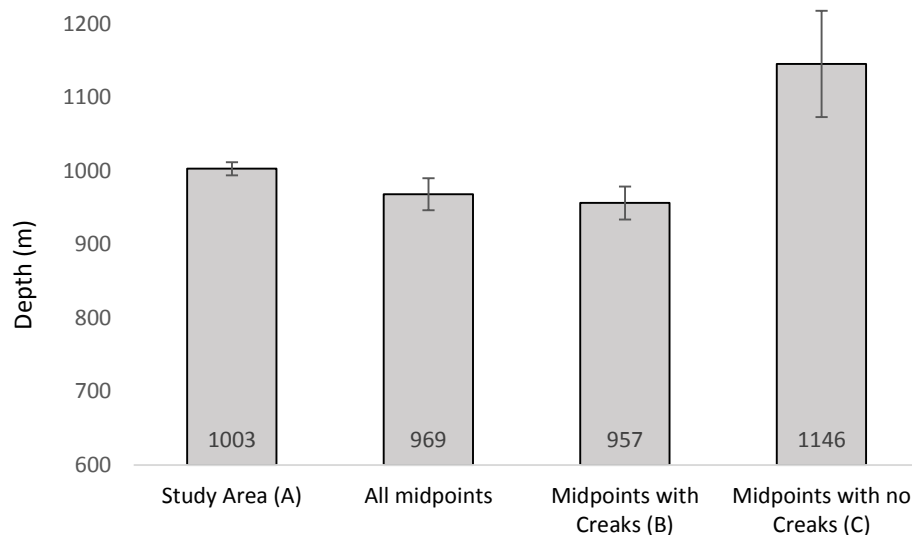


Figure 5.3 – Comparison of mean depth (m) between the study area and those associated with midpoint observations; including dives with and without creak presence. Capital letters depict significant differences.

5.3.3. Fisheries data and relationship to creaks

During field work (October 2009 - June 2011), local commercial fisheries estimated catches of 231 tonnes of fish (c. 11 tonnes per month) from an area covering all whale observations plus an external buffer averaging about 4.8 km (Figure 5.4). Catches included seven species of bony fish and twelve species of sharks. Almost all (98%) events used nets, including set-nets, drift-nets and pair-set nets, which caught 96% of the total estimated weight captured. Trawling, long-lining and other fishing methods accounted for the remainder.

Bony fish and sharks accounted for 41% and 59% of all the fishing events and 60% and 40% of the estimated captures by weight, respectively. Within bony fish catches, groper/bass (which were combined in the MPI data) and ling species accounted for 98% of all fishing events and 99.9% of estimated captures by weight, from which groper/bass represented roughly 53%, both as a percentage of fishing events and captures by weight.

There was a significant positive correlation between the fishing events (FE) of all fisheries (Figure 5.4) and the number of midpoints (M) with presence of creaks ($r=0.79$, $Df=10$, $p=0.002$), as well as with the number of midpoint creaks, MC, ($r=0.72$, $Df=10$, $p=0.008$). Fishing location (FL) was also positively correlated with the number of midpoints with presence of creaks ($r=0.70$, $Df=10$, $p=0.011$), as well as with the number of midpoint creaks ($r=0.74$, $Df=10$, $p=0.006$).

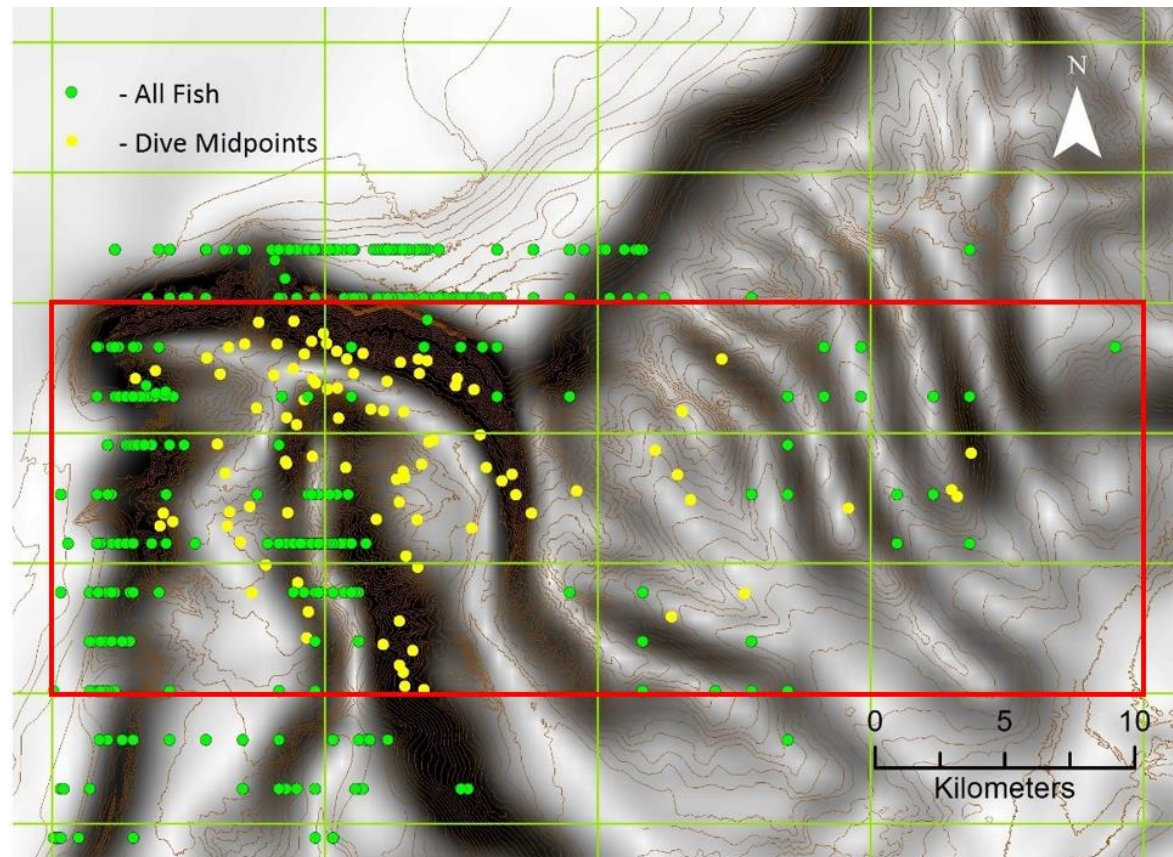


Figure 5.4 – ‘All fish’ (green dots) grid representation with dive midpoints (yellow dots). Each of the 12 cells highlighted in the red bounding box has an approximate area of 51 km². The light green lines represent the grid boundaries. Geographic Coordinate System: WGS198; Projection: Mercator41Swgs.

However, using only bony fish captures (Figure 5.5), no significant correlations were found: FE and creak presence ($r=0.74$, $t=1.578$, $Df=2$, $p=0.255$); FE and MC ($r=0.58$, $t=1.019$, $Df=2$, $p=0.415$); FL and M ($r=0.65$, $t=1.199$, $Df=2$, $p\text{-value}=0.353$); FL and MC ($r=0.47$, $t=0.7502$, $Df=2$, $p\text{-value}=0.531$).

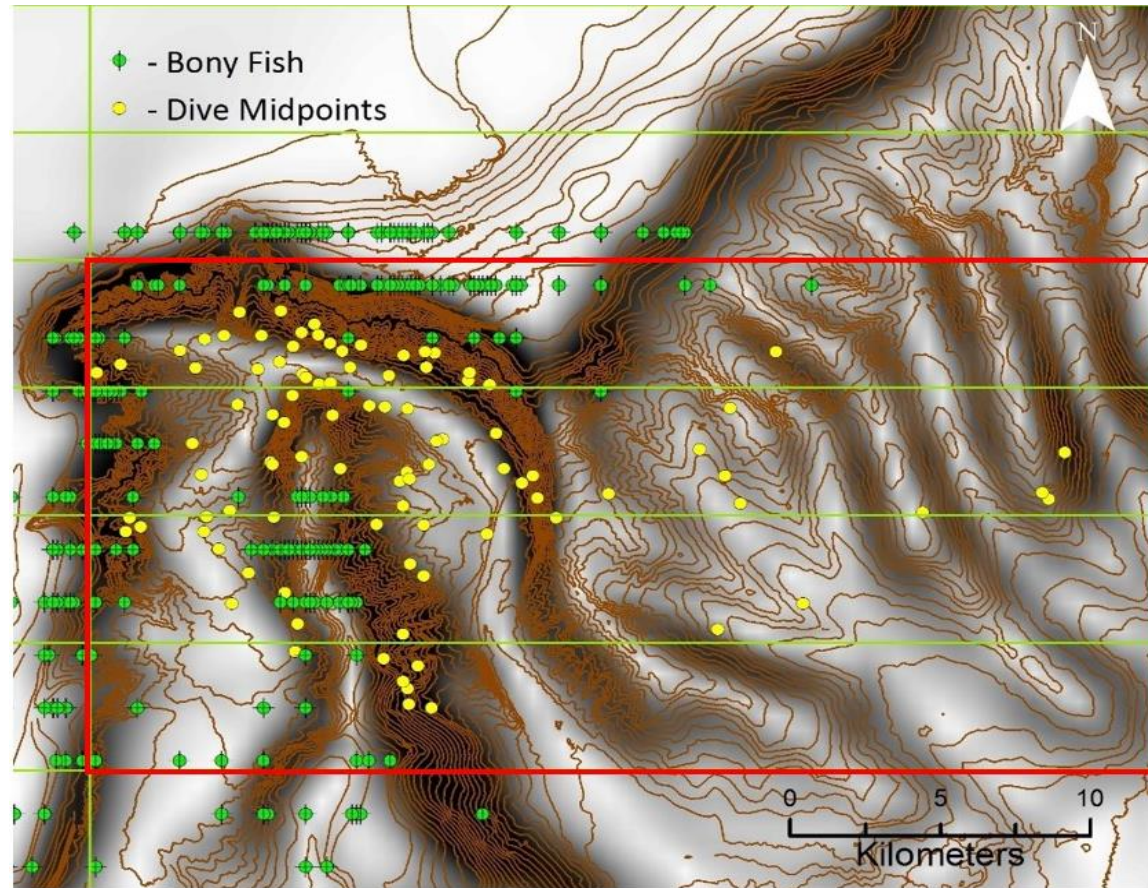


Figure 5.5 – ‘Bony fish’ (green dots) grid representation with dive midpoints (yellow dots). Each of the four cells highlighted in the red bounding box has an area of c. 164 km². The light green lines represent the grid boundaries. Geographic Coordinate System: WGS198; Projection: Mercator41Swgs.

5.4. Discussion

To date, my study on 95 dive cycles of 14 sperm whales represents the most complete dataset of male creaks ($n=741$) measured worldwide. Here, I found an average of 7.8 creaks per dive, with a mean creak duration of 27.1 s. I also observed an unusual number of very long creaks, with the longest lasting 5.6 min. Bottom slope, depth and proximity to commercial fisheries had a significant effect on sperm whale location when producing creaks. Compared with other study areas around the world, the long creaks and lower creak rates per dive observed in my study suggest that whales in Kaikoura may follow a strategy based on fewer but larger and/or more nutritious prey compared to other areas.

5.4.1. Creak characteristics

While a creak is generally identified by a rapid increase in the number of regular clicks (often a doubling of ICI repetition rates over two consecutive regular clicks (Fais et al. 2015)), researchers have used different thresholds. Studies using acoustic tags allow researchers to precisely identify their ICI threshold (Madsen et al. 2002a, Miller et al. 2004a), but using PAM this is not always possible, as fainter creak clicks are not always detectable (Teloni 2005). As I could not always detect my end of creak based on ICI threshold, I instead used the first regular click after a creak, and as a consequence my creak duration may have been overestimated by 2-10 s, compared to studies using tags. This extra time corresponds to a short silent period that occurs after a creak and before resuming regular searching clicks (Gordon 1987, Jaquet et al. 2001, Miller et al. 2004a). Nevertheless, the creak duration found here (27.1 s) was, irrespective of the different end of creak definitions, longer than those found from males in other regions (Madsen et al. 2002b, Mullins et al. 1988). This includes the only other male-only foraging ground where studies have been conducted on a regular basis, the Bleik canyon off Norway, where tag data on four males found a mean creak duration of 10.3 s from 74 complete dives (Teloni et al. (2008). Off Kaikoura, Jaquet and colleagues (2001) investigated creaks - which they defined as ICIs < 0.2 s - using PAM, finding a mean creak duration of 15.65 s ($n=376$). Given the different definitions used, compared with the results from Norway (Teloni et al. 2008), these results exhibit a closer match to my results, although they are still shorter. Creak rates reported by Teloni et al. (2008) are comparable to those found here (10 creaks per dive; $SD=11$; range: 1-46 vs. 7.8; $SD=7.9$; range: 0-50, respectively). Given the differences in creak duration, it is possible that the prey types targeted by whales foraging off

Kaikoura require longer chasing times, perhaps due to preying on more nimble or larger prey, or, although less likely, that the smaller, younger (Dawson et al. 1994, Miller et al. 2013b), and hence potentially less experienced males from Kaikoura take longer to catch the same prey type compared to those of the larger males from Norway (Lettevall 2003, Lettevall et al. 2002). However, as Teloni et al. (2008) collected their data over a single summer month, fluctuations in prey availability (Waluda and Pierce 1998) could also have favoured the abundance of a prey type requiring less chasing time.

Because it is not known whether sperm whales catch a single prey for every creak they make, attempts have been made to establish a relationship between the number of creaks and the estimated feeding requirements for this species (Gordon 1987, Miller et al. 2004a). These attempts assume that every creak led to a successful prey capture and results have been consistent with the predicted feeding requirements of sperm whales. Lockyer (1981) estimated sperm whales' daily food requirement to be 3% of their body weight, based on their heart weight and nutritional value of cephalopod prey. I used size estimates from 33 whales from Kaikoura, from which 32 were recorded over multiple field seasons (Table I in Miller et al. (2013b)) to estimate an average individual size for this feeding ground. I then used Lockyer's (1976) equation ($1.25 * 0.0196 * length^{2.74}$) to estimate body mass from body length, where 1.25 is a multiplier that accounts for blood loss for animals weighted in parts (during whaling), which was removed since these estimates are from living animals. I estimated the mean number of creaks per diving h by dividing the total number of creaks from all animals (741) by the total diving time (64.52 h) from my data. The proportion of the day that sperm whales spent diving was calculated from the relationship between time spent at the surface (13.4 h) and that spent diving, assuming sperm whales from Kaikoura forage equally during day and night (Gordon 1987, Whitehead and Weilgart 1991). Thus, the number of creaks produced daily was estimated at about 227. In order to match the 3% prediction, average prey size in Kaikoura was estimated to be c. 4 kg, which is about three times higher than estimates for the Gulf of Mexico (0.8 kg) and twice those for the Mediterranean (2.3 kg) (Miller et al. 2004a), which were, according to the authors, generally within the range of sizes of typical squid prey consumed by sperm whales worldwide (Whitehead 2003). If we take into account that whales from the Gulf of Mexico were estimated to weigh and measure about 10 t/10 m and those from the Mediterranean about 25 t/12 m (Miller et al. 2004b), the estimated weight and size from the whales at Kaikoura of 29.6 t/14.4 m seems in line with previous estimates. The estimated wet weight of cephalopod prey sampled from stomach contents of 36 stranded sperm whales along the coast of Tasmania, Australia, ranged from 2.7 – 110233.1 g (mean \pm SD = 828.3 \pm 3073.6

g) (Evans and Hindell 2004), while the stomach contents from males caught in the Cook Strait region showed small to medium size (1-4 ft.) squid, weighing 0.5-3 kg, with a mean of 2.58 kg, and an average fish weight of 6.5 kg (means calculated from available data on whale 17, 64, 80, 90, 120, 154, 33, 36; pages 161- 162; Gaskin and Cawthorn (1967)). Evans and Hindell's (2004) prey average of 0.828 kg are well below mine, however, the resulting average weight per prey between squid and fish from Gaskin and Cawthorn (1967), of 4.54 kg $((2.58 + 6.5) / 2)$ is in accordance with the estimated average prey size made here, and from a closer geographical area.

The estimated Kaikoura average prey size, coupled with longer-than-average creaks and an apparent lack of seasonal variation in creak duration, suggests that sperm whales in this area may regulate the bulk of their diet according to the seasonal fluctuations of different fish species, while opportunistically consuming squid. This observation is supported by findings of different fish species found present at specific times of the year, and the constant presence of squid within the analysed stomach contents of whales from this region (Gaskin and Cawthorn 1967). Additionally, the suggested relationship between creak duration and prey type, where longer creaks are thought to target fish (Miller et al. 2004a, Teloni et al. 2008), and the surface feeding observations found in this study, all add support to the idea that sperm whales foraging over the Kaikoura canyon have a fish-focussed diet. Furthermore, longer creak averages from two males thought to be foraging on fish along the Nova Scotia shelf (26.8 s measured from 17 creaks and 61 s from 5 creaks) also support this interpretation (Mullins et al. 1988).

Several studies on female family units that reveal information on creaks did not analyse complete dive cycles and only showed rough creak durations, or their range (Gordon 1987, Weilgart 1990, Whitehead and Weilgart 1990, Whitehead and Weilgart 1991). However, Miller and colleagues' (2004a) and Watwood and colleagues' (2006) large datasets, acquired using acoustic tags, show a remarkable difference in creak rates and duration compared with my results and those from other males (Jaquet et al. 2001, Madsen et al. 2002b, Miller et al. 2013a, Mullins et al. 1988, Teloni et al. 2008). Based on creak rates and its duration, respectively, females were found to encounter over twice as much prey per dive and spend less than a third of their time chasing prey (Miller et al. 2004a, Watwood et al. 2006), compared to males from this study. The different creak pattern between sexes is possibly related to different physiological needs (Whitehead 2003), where females seem to adopt a more consistent strategy of targeting a higher number of smaller and less nutritional prey (i.e. cephalopods) (Clarke 1980, Clarke 1986), which require a shorter chasing time, as opposed to males, which

seem to consume a greater range of food, investing on higher nutritional and/or larger prey (i.e. fish) (Best 1979, Whitehead 2003).

5.4.2. *A note on long creaks*

On several occasions during long series of fast clicks associated with surface feeding, the ICI oscillations above and below the creak definition (i.e. ≤ 0.1 s) resulted in labelling multiple creaks. It is likely that these 'consecutive creaks' were all part of the same prey pursuit, for which the term 'creak' was intended. This may have resulted in an underestimation of the real creak duration (as a feeding attempt) in some instances. ICI variation during surface feeding strongly suggests a predator-prey interaction where a fast-moving prey gains distance from the whale to later lose it, as pursuit predation works in other species (Sih 1984, Wilson et al. 2013), which coupled with fish prey surface-feeding behaviour (Miller et al. 2013a), does not support the "passive luring" hypothesis (Beale 1839) where sperm whales wait still and suck in their prey (Werth 2004) without the use of their teeth. Fish were confirmed as the target species on three of these long creak observations.

Males may diversify their diet during dispersal, including consumption of a larger amount of fish, to achieve the nutritional requirements necessary to grow and become competitive when returning to feeding grounds (Whitehead 2003). However, how a slow-moving whale (Watkins et al. 1993) can outmanoeuvre fast moving prey, such as kingfish (which has been identified in stomach contents (Gaskin and Cawthorn 1967) as well as during surface feeding off Kaikoura (Miller et al. 2013a)), remains a mystery. Conversation exchanges with several helicopter pilots operating over the Kaikoura canyon has resulted in the following written testimony by the commercial helicopter pilot Dominic O'Rourke (2010):

"...The whale was coming up vertically with up to 1/3 of its body out of the water trying to catch a large kingfish (1.5 meters approx.) in its mouth. The whale missed it and ducked down to have another go and missed again, after about 3 goes with a very wide open jaw each time the king fish swam away steadily and close to the surface, but quite slow for a kingfish - N [distance] from the whale up to about 12 meters, the whale gave chase, and after about 6 seconds the fish seemed to swim in a much slower and more disorientated way, the fish circled slowly back towards the whale and was now not swimming vertical but listing to the right quite sharply and slowing..."

The whale closed on the fish's location and again positioned itself so that it could come up fairly vertical on the fish from below but also more on its back than normal so the jaw was the closest thing to the surface. It then had again about 3 attempts at getting the "stunned" fish which was at this point not swimming away and seemed to be struggling to move to stay out of the jaw. The whale seemed slightly clumsy and then did finally get the fish and swallowed it whole..."

The other times I and other pilots here have seen this surface feeding it has been very much the same scenario with the same outcome of the whale eventually getting the fish after multiple attempts.”

Although estimates (including the one made in the current study) of daily prey consumption by sperm whales have assumed that creak rates reflect the number of successful prey captures (Gordon 1987, Miller et al. 2004a), O’Rourke’s observations, and those of other pilots operating off Kaikoura (pers. comm. Aaron Peacock), indicate that for fast moving fish, sperm whales may need up to six or seven attempts before they capture the prey.

The proportion of longer and shorter creaks measured here was not analysed in detail, but it is safe to say that creak repertoire was not dominated by long creaks (e.g., > 100 s). A possible explanation for how these slow moving whales succeed in preying on fast moving fish is that the directionality and extreme source levels of both regular and creak clicks, which include the loudest known biological sound (Møhl et al. 2003, Møhl et al. 2000), may affect the Mauthner cells connected to the lateral line of teleost fish (Eaton and Hackett 1984, Popper and Higgs 2009). Mauthner cells are critical elements of an escape reflex induced by abrupt threatening events, but which is inhibited by being repeatedly submitted to sound (Korn and Faber 2005). While this hypothesis remains to be tested, echolocation could have an effect on fish behaviour, which, coupled with physical pursuit, may culminate in the exhaustion of the fish, helping sperm whales (and maybe other odontocetes) capture their prey. Possibly supporting this are further anecdotes from helicopter pilots. One observation of surface feeding off Kaikoura describes a male sperm whale approaching a two m long shark and using its jaw to snap it in two in a single attempt, after which it manoeuvred to pick up half of the shark, leaving the other half behind (pers. comm. D. O’Rourke). Yet another pilot declared seeing several surface feeding events per year, where each event last about 12 to 15 min and taking about six attempts for a whale to catch a single fish prey (pers. comm. Aaron Peacock). These observations and the surface fish-feeding events observed during field work highlight the need for caution when estimating food consumption of sperm whales based on creak rates, and provide some evidence that long creaks are used for targeting highly manoeuvrable fish, rather than squid.

5.4.3. *Habitat features associated with creaks*

Whales are not located randomly during foraging, as both slope and depth are correlated with whale location within the study area. Specifically, steep gradients and shallower depths were associated with creak production. In contrast, locations in which dives without creak occurrence were made, representing only 6.3% of all dives analysed, were deeper and had lower slope gradients. Since male sperm whales in this study were always found foraging, it is possible that the absence of creaks associated with lower slopes and higher depths; i.e. the canyon valleys, results from individuals foraging opportunistically in between target areas (higher slopes) (Fais et al. 2015). This possibility is further supported by research showing that sperm whales follow a methodical procedure (Laplanche et al. 2005), using foraging success as well as click echo information gathered from previous dives for planning later ones (Fais et al. 2015).

Even though the depth and slope associated with midpoints show that the whales are particular about these bathymetric features during foraging off Kaikoura, the exact preferred values are likely different from those described here, since midpoints don't necessarily represent the precise 'preferred' slope and depth values associated with creaks. Whales moved about 2 km between surfacings; thus while swimming over steep slope areas (where depth also changes at fast rates), a short distance travelled may result in a significant change in slope and depth. Knowing the exact location of creaks (e.g., through the use of tags) would likely increase the accuracy of results in terms of absolute slope and depth values associated with creak presence vs. those where no creaks were recorded.

5.4.4. *Fisheries data and relationship to creaks*

Creak event locations and commercial fisheries targeting fish species that sperm whales consume were, for bony fish and sharks combined, spatially correlated. While the accuracy of analysis may have been affected by the low resolution of the fisheries data available, the results are consistent with the longer than average creaks found in the present study. The analysis in which sharks were included (compared to that only including bony fish) suggests that sharks may be a regular prey option for sperm whales foraging in this area. Sharks were, after groper and ling species, the most abundant catch during the study period.

Worldwide, male sperm whales are known to consume sharks of different species (Gaskin and Cawthorn 1967, Stewart et al. 2002). Two alternatives are possible given my analyses: that sperm whales here, too, are targeting sharks, or that the proximity of creaking whales to fishing locations is indirectly related to shark abundance and that sperm whales are targeting bony fish, or, indeed squid, which may also be associated with areas in which bony fish are found. Squid are the most common food item found in sperm whale stomachs worldwide (Clarke 1980, Clarke 1996). Arrow squid (*Nototodarus sloanii*) and *Moroteuthis* sp., in particular, are the most abundant squid species in Kaikoura and nearby areas (Anderson et al. 1998), and are found regularly in sperm whale' stomachs from this region (Gaskin and Cawthorn 1967).

5.4.5. *Conclusions*

In summary, male sperm whales foraging over the Kaikoura canyon produce the longest creak duration averages found to date. Visual observations of fish prey were associated with very long creaks, from which ICIs suggest pursuit predation of fast-moving prey, as opposed to suction feeding. Given the estimated average prey size based on daily food requirements and creak rates, my results suggest that sperm whales may regulate the bulk of their diet according to the seasonal fluctuations of different fast-moving fish species in this area. Further support to this hypothesis is that slope, depth and proximity to commercial fisheries targeting fish species (not cephalopod) consumed by sperm whales were found to be significant factors affecting sperm whales spatial distribution in the Kaikoura canyon.

5.5. References

- Anderson, O. F., N. W. Bagley, R. J. Hurst, M. P. Francis, M. R. Clark, and P. J. McMillan. 1998. Atlas of New Zealand fish and squid distributions from research bottom trawls. NIWA Technical Report 42. 303 pp.
- Beale, T. 1839. The natural history of the sperm whale. John van Voorst, London.
- Best, P. B. 1979. Social organization in sperm whales, *Physeter macrocephalus*. Pages 227-289 in H. E. Winn and B. L. Olla, editors. Behavior of Marine Animals. Springer US.
- Best, P. B. 1999. Food and feeding of sperm whales *Physeter macrocephalus* off the west coast of South Africa. South African Journal of Marine Science **21**(1):393-413.
- Childerhouse, S. J., S. M. Dawson, and E. Slooten. 1995. Abundance and seasonal residence of sperm whales at Kaikoura, New Zealand. Canadian Journal of Zoology **73**(4):723-731.
- Clarke, M. R. 1980. Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. University of California Press, Berkeley, 324 pp.
- Clarke, M. R. 1986. Cephalopods in the diets of odontocetes. Pages 281-321 in M. M. Bryden and R. Harrison, editors. Research on dolphins. Clarendon Press, Oxford.
- Clarke, M. R. 1996. Cephalopods as prey. III. Cetaceans. Philosophical Transactions of the Royal Society of London B: Biological Sciences **351**(1343):1053-1065.
- Clarke, M. R., H. R. Martins, and P. Pascoe. 1993. The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. Philosophical Transactions of the Royal Society of London B: Biological Sciences **339**(1287):67-82.
- Clarke, M. R., and P. L. Pascoe. 1997. Cephalopod species in the diet of a sperm whale (*Physeter catodon*) stranded at Penzance, Cornwall. Journal of the Marine Biological Association of the UK **77**(4):1255-1258.
- Dawson, S. M., E. Slooten, and O. Jake. 1994. Distribution, abundance and population structure of sperm whales at Kaikoura. WWF-NZ, Wellington.
- Douglas, L. A., S. M. Dawson, and N. Jaquet. 2005. Click rates and silences of sperm whales at Kaikoura, New Zealand. Journal of the Acoustical Society of America **118**(1):523-530.
- Eaton, R. C., and J. T. Hackett. 1984. The role of the Mauthner cell in fast-starts involving escape in teleost fishes. Pages 213-266 in R. C. Eaton, editor. Neural mechanisms of startle behavior. Springer US, Boston.
- Evans, K., and M. A. Hindell. 2004. The diet of sperm whales (*Physeter macrocephalus*) in southern Australian waters. ICES Journal of Marine Science **61**(8):1313-1329.
- Fais, A., N. Aguilar de Soto, M. P. Johnson, C. Pérez-González, P. J. O. Miller, and P. T. Madsen. 2015. Sperm whale echolocation behaviour reveals a directed, prior-based search strategy informed by prey distribution. Behavioral Ecology and Sociobiology **69**(4):663-674.

- Gaskin, D. E., and M. W. Cawthorn. 1967. Diet and feeding habits of the sperm whale (*Physeter catodon* L.) in the Cook Strait region of New Zealand. *New Zealand Journal of Marine and Freshwater Research* **1**(2):156-179.
- Gordon, J. C. D. 1987. Sperm whale groups and social behaviour observed off Sri Lanka. PhD thesis. University of Cambridge, Cambridge, England.
- Griffin, D. R., F. A. Webster, and C. R. Michael. 1960. The echolocation of flying insects by bats. *Animal Behaviour* **8**(3-4):141-154.
- Jaquet, N., S. Dawson, and L. Douglas. 2001. Vocal behaviour of male sperm whales: why do they click? *Journal of the Acoustical Society of America* **109**(5):2254-2259.
- Jaquet, N., S. Dawson, and E. Slooten. 2000. Seasonal distribution and diving behaviour of male sperm whales off Kaikoura: foraging implications. *Canadian Journal of Zoology* **78**(3):407-419.
- Judkins, H. L., S. Arbuckle, M. Vecchione, L. Garrison, and A. Martinez. 2015. Cephalopods in the potential prey field of sperm whales (*Physeter macrocephalus*) (Cetacea: Physeteridae) in the northern Gulf of Mexico. *Journal of Natural History* **49**(21-24):1267–1280.
- Kalko, E. K. V. 1995. Insect pursuit, prey capture and echolocation in pipistrelle bats (Microchiroptera). *Animal Behaviour* **50**(4):861-880.
- Kasuya, E. 2001. Mann–Whitney U test when variances are unequal. *Animal Behaviour* **61**(6):1247-1249.
- Kawakami, T. 1980. A review of sperm whale (*Physeter macrocephalus*) food. *Scientific Reports of the Whales Research Institute, Tokyo* **32**:199-218.
- Korn, H., and D. S. Faber. 2005. The Mauthner cell half a century later: a neurobiological model for decision-making? *Neuron* **47**(1):13-28.
- Laplanche, C., O. Adam, M. Lopatka, and J.-F. Motsch. 2005. Male sperm whale acoustic behavior observed from multipaths at a single hydrophone. *Journal of the Acoustical Society of America* **118**(4):2677-2687.
- Lettevall, E. 2003. Abundance, association and movement within discrete populations of sperm whales, *Physeter macrocephalus*. PhD thesis. Göteborg University, Göteborg, Sweden.
- Lettevall, E., C. Richter, N. Jaquet, E. Slooten, S. Dawson, H. Whitehead, J. Christal, and P. M. Howard. 2002. Social structure and residency in aggregations of male sperm whales. *Canadian Journal of Zoology* **80**(7):1189-1196.
- Lockyer, C. 1981. Estimates of growth and energy budget for the sperm whale, *Physeter catodon*. *FAO Fisheries Series* **5**:489-504.
- Madsen, P. T., R. Payne, N. U. Kristiansen, M. Wahlberg, I. Kerr, and B. Møhl. 2002a. Sperm whale sound production studied with ultrasound time/depth-recording tags. *Journal of Experimental Biology* **205**(Pt13):1899-1906.

- Madsen, P. T., M. Wahlberg, and B. Møhl. 2002b. Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and communication. *Behavioral Ecology and Sociobiology* **53**(1):31-41.
- Madsen, P. T., M. Wilson, M. P. Johnson, R. T. Hanlon, A. Bocconcelli, N. Aguilar de Soto, and P. L. Tyack. 2007. Clicking for calamari: toothed whales can echolocate squid *Loligo pealeii*. *Aquatic Biology* **1**:141-150.
- Martin, A. R., and M. R. Clarke. 1986. The diet of sperm whales (*Physeter macrocephalus*) captured between Iceland and Greenland. *Journal of the Marine Biological Association of the UK* **66**(4):779-790.
- Mendes, S., N. Jason, R. J. Reid, A. F. Zuur, and G. J. Pierce. 2007. Stable carbon and nitrogen isotope ratio profiling of sperm whale teeth reveals ontogenetic movements and trophic ecology. *Oecologia* **151**(4):605-615.
- Miller, B. S. 2010. Acoustically derived growth rates and three-dimensional localisation of sperm whales (*Physeter macrocephalus*) in Kaikoura, New Zealand. PhD thesis. University of Otago, Dunedin, New Zealand.
- Miller, B. S., S. Dawson, and R. Vennell. 2013a. Underwater behavior of sperm whales off Kaikoura, New Zealand, as revealed by a three-dimensional hydrophone array. *Journal of the Acoustical Society of America* **134**(4):2690-2700.
- Miller, B. S., A. Growcott, E. Slooten, and S. M. Dawson. 2013b. Acoustically derived growth rates of sperm whales (*Physeter macrocephalus*) in Kaikoura, New Zealand. *Journal of the Acoustical Society of America* **134**(3):2438-2445.
- Miller, P. J. O., M. P. Johnson, and P. L. Tyack. 2004a. Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. *Proceedings of the Royal Society of London B: Biological Sciences* **271**(1554):2239-2247.
- Miller, P. J. O., M. P. Johnson, P. L. Tyack, and E. A. Terray. 2004b. Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. *Journal of Experimental Biology* **207**(11):1953-1967.
- Møhl, B., M. Wahlberg, P. T. Madsen, A. Heerfordt, and A. Lund. 2003. The monopulsed nature of sperm whale clicks. *Journal of the Acoustical Society of America* **114**(2):1143-1154.
- Møhl, B., M. Wahlberg, P. T. Madsen, L. A. Miller, and A. Surlykke. 2000. Sperm whale clicks: directionality and source level revisited. *Journal of the Acoustical Society of America* **107**(1):638-648.
- Mullins, J., H. Whitehead, and L. S. Weilgart. 1988. Behaviour and vocalizations of two single sperm whales, *Physeter macrocephalus*, off Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences* **45**(10):1736-1743.
- Paul, L. J. 2002. A description of the New Zealand fisheries for the two groper species, hapuku (*Polyprion oxygeneios*) and bass (*P. americanus*). Ministry of Fisheries, Wellington, New Zealand.

- Popper, A. N., and D. M. Higgs. 2009. Fish: hearing, lateral lines (mechanisms, role in behavior, adaptations to life underwater). Pages 476-482 in J. H. Steele, K. K. Turekian, and S. A. Thorpe, editors. Encyclopedia of Ocean Sciences. Academic Press, Oxford, UK.
- R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rice, D. W. 1989. Sperm whale, *Physeter macrocephalus* (Linnaeus, 1758). Pages 177-233 in S. H. Ridgway and R. Harrison, editors. Handbook of Marine Mammals. Academic Press, London, UK.
- Sagnol, O. J. Y., C. Richter, L. H. Field, and F. Reitsma. 2014. Spatio-temporal distribution of sperm whales (*Physeter macrocephalus*) off Kaikoura, New Zealand, in relation to bathymetric features. New Zealand Journal of Zoology **41**(4):234-247.
- Shapiro, S. S., and M. B. Wilk. 1965. An analysis of variance test for normality (complete samples). Biometrika **52**(3-4):591-611.
- Sih, A. 1984. The behavioral response race between predator and prey. The American Naturalist **123**(1):143-150.
- Smith, S. C., and H. Whitehead. 2000. The diet of Galápagos sperm whales *Physeter macrocephalus* as indicated by fecal sample analysis. Marine Mammal Science **16**(2):315-325.
- Stewart, B. S., P. J. Clapham, J. A. Powell, and R. R. Reeves. 2002. Guide to marine mammals of the world. National Audubon Society field guides. Knopf, New York, 528 pp.
- Teloni, V. 2005. Patterns of sound production in diving sperm whales in the northwestern Mediterranean. Marine Mammal Science **21**(3):446-457.
- Teloni, V., M. P. Johnson, P. J. O. Miller, and P. T. Madsen. 2008. Shallow food for deep divers: dynamic foraging behavior of male sperm whales in a high latitude habitat. Journal of Experimental Marine Biology and Ecology **354**(1):119-131.
- Van der Linde, M. 2010. Long-term monitoring of sperm whales in Kaikoura, New Zealand: data-management, abundance, and population dynamics. MSc thesis. University of Otago, Dunedin, New Zealand.
- Waluda, C. M., and G. J. Pierce. 1998. Temporal and spatial patterns in the distribution of squid *Loligo* spp. in United Kingdom waters. South African Journal of Marine Science **20**(1):323-336.
- Watkins, W. A., M. A. Daher, K. M. Fristrup, T. J. Howald, and G. Notarbartolo di Sciara. 1993. Sperm whales tagged with transponders and tracked underwater by sonar. Marine Mammal Science **9**(1):55-67.
- Watwood, S. I., P. J. O. Miller, M. P. Johnson, P. T. Madsen, and P. L. Tyack. 2006. Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). Journal of Animal Ecology **75**(3):814-825.

- Weilgart, L. S. 1990. Vocalizations of the sperm whale (*Physeter macrocephalus*) off the Galápagos Islands as related to behavioral and circumstantial variables. PhD thesis. Dalhousie University, Halifax, Nova Scotia.
- Werth, A. J. 2004. Functional morphology of the sperm whale (*Physeter macrocephalus*) tongue, with reference to suction feeding. *Aquatic Mammals* **30**(3):405-418.
- Whitehead, H. 1994. Delayed competitive breeding in roving males. *Journal of theoretical biology* **166**(2):127-133.
- Whitehead, H. 2003. Sperm whales: social evolution in the ocean. University of Chicago Press.
- Whitehead, H., and L. Weilgart. 1990. Click rates from sperm whales. *Journal of the Acoustical Society of America* **87**(4):1798-1806.
- Whitehead, H., and L. Weilgart. 1991. Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. *Behaviour* **118**(3-4):275-296.
- Wilson, A. M., J. C. Lowe, K. Roskilly, P. E. Hudson, K. A. Golabek, and J. W. McNutt. 2013. Locomotion dynamics of hunting in wild cheetahs. *Nature* **498**(7453):185-189.

6. General discussion

Marine mammals produce sounds to communicate identity and convey information about their location (Richardson et al. 1995). Their communication may also serve to coordinate group movements, reveal territorial or reproductive state or the presence of predators, or may be used to locate food resources (Richardson et al. 1995). Moreover, odontocetes cetaceans use echolocation to gather further information, within and beyond their visual range, including finding and identifying prey, objects, conspecifics and bathymetry (Au 1993, Fais et al. 2015, Herman et al. 1998).

Sperm whales are born into established social units with a complex structure, which includes long-term bonds (Whitehead 2003). Developing strategies of group living, including the ability to maintain contact with other group members during coordinated foraging and socializing, as well as learning the vocal repertoire of the clan to which they belong (i.e. codas), are fundamental skills for their survival (Gero et al. 2016, Whitehead 2003). However, during puberty, males disperse from their natal units (Mendes et al. 2007, Pinela et al. 2009), which results in a different social organisation among dispersing and dispersed males (Best 1979).

At higher latitude male-only grounds, dispersed males are often found in aggregations where they maximise foraging time, which in their natal units is otherwise used for socialising (Whitehead 2003). Based on a general absence of physical close proximity between dispersed males in these areas, these whales have traditionally been considered solitary animals (Lettevall et al. 2002, Madsen et al. 2002b). Whether the large-scale spatial and temporal movement patterns of dispersed males is a result of male coordination (Christal and Whitehead 1997), or whether individuals congregate by following similar foraging cues, has not been clarified (Brown and Orians 1970, Lettevall et al. 2002, Whitehead 2003).

Slow clicks are vocalisations produced only by males. In the male foraging grounds off Kaikoura (Jaquet et al. 2001) and Norway (Oliveira et al. 2013), slow clicks following consistent temporal and diving-phase patterns are heard on a daily basis (Chapter 2). However, slow clicks were first described from recordings made at female breeding grounds, by Gordon (1987), who called them ‘Clangs’, and by Weilgart and Whitehead (1988), who found an association between slow clicks and the presence of mature males. However, slow click sequences recorded in breeding grounds may follow different patterns from those recorded in male-only regions. At breeding grounds, males seem to slow click for extended periods while close to, or at the surface, suggesting a function of vocal display used in competition and/or to

attract females (Weilgart and Whitehead 1988, Whitehead 1993). While the function of slow clicks is still unresolved, and may differ depending on context, their sound properties favour a function for long-range communication (Gordon 1987, Madsen et al. 2002b, Oliveira et al. 2013, Weilgart and Whitehead 1988) over echolocation (Goold 1999, Gordon 1987, Jaquet et al. 2001, Mullins et al. 1988, Tyack and Clark 2000).

In this study, I used a towed hydrophone array and photo-identification data from individually-tracked whales during complete foraging dives, to further understand the function of slow clicks in the Kaikoura canyon male foraging ground. I investigated the presence and number of slow clicks as a function of other acoustically-detected whales in the area. I also tested a possible echolocation function for slow clicks, and examined their structure, including their centre frequency, waveform, and the occurrence of multiple pulses within clicks (which carry body size-related information in regular echolocating clicks) to examine their relationship to the total body length of individuals. The pulse structure and amplitude of slow clicks were analysed in relation to directionality. Codas and slow clicks used by a pair of males synchronising at the surface, and during a complete dive cycle, were also examined in terms of their spectral characteristics, waveform and coda duration. Finally, I looked at the feeding vocalisation (creaks) rates, their duration, and the relationship between their presence, the bathymetry and the commercial fisheries within the underwater canyon off Kaikoura.

I found that male sperm whales foraging off Kaikoura tend to produce more slow clicks as the number of other acoustically detected males increased (Chapter 2). If males use slow clicks to communicate foraging location (Madsen et al. 2002b, Oliveira et al. 2013), an average of 5.8 clicks per bout (Chapter 3) and a rate of increase of 0.2 bouts for every additional whale detected in the area (Chapter 2) suggests that a single additional slow click is produced per every additional whale present. My hypothesis that slow-clicking whales adjust their body posture to take into account the beam pattern of slow clicks (Chapter 3) may help to explain why only a single slow click may be sufficient to update other whales on the foraging location of a given individual. If the vocaliser directs its slow click beam towards the desired target/individual, this may facilitate the assessment of distance between individuals, and hence help whales to optimise the use of space, by taking into account each other's location. The targeted whale could additionally assess individual features of the slow clicking whale from information contained in the waveform of slow clicks, such as the inter-pulse interval found in most slow clicks, and from their amplitude and/or frequency content (Chapter 3). Because aggression between males is rarely observed (Whitehead 2003), and was never witnessed in this study, slow clicks could thus function to optimise the relationship between foraging space

available and total number of foraging individuals (Pyke 1984). The Kaikoura canyon is among the most productive deep-sea regions in the world (De Leo et al. 2010) and lies in a relatively enclosed area. The larger nutritional demand of males, compared with that of the smaller females (Best 1979, Teloni et al. 2008), coupled with my finding that males in this region are likely targeting fewer but larger and/or more nutritious prey compared to other areas (Chapter 5), may explain the need for a detailed spatial awareness between foraging individuals.

There is a general consensus for a lack of territoriality among sperm whales, based on their large and overlapping home ranges and on their patchy food distribution, which is spatiotemporally highly variable (Best 1979, Waluda and Pierce 1998, Whitehead 2003). Additionally, the energy costs associated with defending extended foraging areas, especially in a three-dimensional environment like the ocean, is likely unsustainable (Brown and Orians 1970, Whitehead 2003). Thus, while my results fit within the hypothesis that males use slow clicks for establishing foraging areas (Madsen et al. 2002b, Oliveira et al. 2013), this is by no means straightforward.

In Chapter 4, I described in detail the acoustic behaviour of a pair of whales observed diving and surfacing in synchrony throughout a foraging dive cycle. The same two individuals (of which one is a well-known ‘local whale’; whale ID 1 known as ‘Manu’) had been previously observed clustering at the surface almost four years prior (Van der Linde 2010). At the ‘start’ of dives the whales produced codas, and at the ‘end’ of the dives they produced slow clicks alternated and/or overlapping with codas, and ‘slow click codas’; the latter possibly being a new coda type produced by males (Chapter 4). Although only based on a single observation, this may suggest that slow clicks in this context had a function that was not agonistic. Indeed, slow clicks here could have been used by the pair of males to aid in individual recognition, since the centre frequency of slow clicks was found to vary between individuals (Chapter 3). The apparent low variability of the centre frequency of slow clicks between different regions, and the fact that I found no association between the centre frequency of slow clicks and the total length of the vocaliser (Chapter 3), suggests however, that at a population level, the centre frequency alone may not be a good signal for individual identification. However, within a limited number of individuals of relatively similar sizes (i.e., bachelor group members of the same age/size range), it is feasible that centre frequency, coupled with the multi-pulse structure present in the waveform of most slow clicks analysed (Chapter 3) and the variations in inter-click intervals (ICI) inherent to slow click bouts (Chapter 2), may, in combination, be a sufficient set of cues by which individuals are identified

(Beecher 1989). In addition, the finding that the same pair of males had been observed in close synchrony almost four years prior, and that other clusters (nine pairs and one trio) were observed during this study, during which slow clicks, codas and coda-creaks were registered during two of these additional observations, provide indirect evidence that males may recognise individual conspecifics. However, this is a single isolated incident, and of course there are numerous unrecorded instances of whales in the region seen in synchrony (pers. comm. Whale Watch Kaikoura). Because no recordings are available from these instances, my hypothesis remains purely speculative.

If slow clicks are used as contact calls, their dive-phase temporal characteristics (Chapter 2) may, like codas, be physiologically affected by depth (Madsen et al. 2002a). This could explain why there is no clear exchange of slow clicks bouts (Lamoni et al. 2013, Oliveira et al. 2013) compared to the coda exchanging within socialising females at, or close to the surface (Schulz et al. 2008). Males may thus have a limited window of opportunity to reply to conspecifics, such that they may only be able to reply above a certain depth, near the surface (Oliveira et al. 2013). Given this conjectural scenario, and assuming a dive-phase delay associated with the exchange of slow click bouts between individuals, slow clicks may, in addition to helping maintaining group cohesion, also aid whales intending to synchronise at the surface (Best 1979, Gaskin 1970, Lettevall et al. 2002). By keeping track of each other's dive cycle phase, males intending to cluster at the surface with other 'group members', could regulate their dive phases to avoid being 'out of phase' when both whales are nearby, thus avoiding having to abort an on-going dive, or delay the start of a new dive. Slow clicks could thus also function to minimise a loss of foraging time associated with close encounters at the surface. In addition, the large distances covered by slow clicks (Madsen et al. 2002b) would provide individuals with greater foraging independence, while maintaining contact with other members of their aggregation/bachelor group. The range at which slow clicks may be detected by conspecifics has been estimated, assuming spherical spreading, at 60 km (Madsen et al. 2002b). My finding that both amplitude and the waveform shape of slow clicks vary considerably within bouts (Chapter 3), which might suggest a defined directionality and adjustment of the body orientation by slow-clicking whales, may have implications on the estimated distances at which sperm whales detect slow clicks. The ability of slow-clicking whales to use directionality in their favour is likely to increase the distance and efficacy of these signals.

Elephants (Proboscidea), whose social structure is remarkably similar to that of sperm whales (Weilgart et al. 1996), are able to distinguish the calls of female family and bond group

members from those of females outside of these categories, and may need to be familiar with contact calls of about fourteen families, including 100 animals, to discriminate these calls (McComb et al. 2000). In marine mammals, a study on long-term social recognition showed that bottlenose dolphins discriminate familiar vocalisations from unfamiliar ones, regardless of sex or duration of association, for as long as twenty years (Bruck 2013). Sperm whale coda repertoires define the highest hierarchy of female social organisation, the ‘vocal clan’, which regulates associations between social units (Whitehead et al. 2012). Individual females show association preferences with other individuals within and across social units for decades (Gero et al. 2015). In establishing bachelor groups comprised of animals of similar ages and sizes (Best 1979, Gaskin 1970, Ohsumi 1971), dispersing males could thus use codas as a group association criterion (Rendell and Whitehead 2003) and develop long-term bonds (Pace et al. 2014) by learning and recognising coda and slow click patterns from other members of the ‘new’ (bachelor) group.

In addition to the advantages of group living (Beauchamp 2005, Whitehead et al. 1991, Wilkinson 1992), the biological significance of long-term associations among dispersed males of the same age/size may be explained by the observed different growth rates found among different age/size animals (Best 1970). This may result in different nutritional requirements or foraging skills between animals of different sizes, promoting animals to join those matching their own development stage. Best (1979) found that nearly two thirds of males from groups of small bachelors were sexually immature. Tomosov (cited in Best 1979, 1975) also observed this trend and noticed a latitude restriction associated with these groups. For example, males are known consume more fish than females, which may require developing ‘fish eating skills’ (Chapter 5). If smaller and less experienced males group with larger and more capable animals foraging in a habitat dominated by fish rather than squid, smaller males may become food deprived as a result of being in the wrong size/age group.

Males of the same age/size may also have a similarly-timed reproductive clock, which would be advantageous if males coordinate migration to and from breeding grounds (Matthews et al. 2001, Rice 1989). The periodicity at which males return to breeding grounds, including their first return, is not known. However, given the extreme sexual dimorphism of the species, size is a determining factor for reproductive success (Best 1979, Whitehead 2003), which should encourage younger males to grow (and become sexually mature) before their first appearance for mating (Whitehead 1994). In this light, it may be advantageous for animals that are not fully grown, including those foraging off Kaikoura (Chapter 3), to keep track of others with similar feeding and sexual requirements.

Congruent with the idea that male sperm whales (although probably not all; Straley et al. 2014) may be in permanent acoustic contact with other males is the consistency of the observations detailing the proximity between males, as well as the definitions of ‘solitary’ males used by different authors analysing whaling data, and the whales themselves. The following quotes are examples that reflect my own experience of over the years and in different ocean basins.

“...females are invariably in schools, whereas males may be in schools or they may be solitary.

These solitary whales were known to the old whalers as 'lone bulls'. When a solitary sperm whale is encountered anywhere at sea, there are usually other solitary individuals in the same area. Captain D. McKenzie (in Maury, 1852, p. 238) said that 'four or five may be as many miles from each other'. I have a similar impression from what I have seen in the Azores and in the Antarctic, and heard from whale-gunners. In the Antarctic I have never encountered solitary sperm whales which were less than about one mile apart.”

(Clarke 1956; p. 278)

“Solitary whales are always large, 45-55 ft (13.8-16.8 m) long, and scattered from 1-10 miles (1.6-16 km) from the nearest neighbour.”

(Gaskin 1970; p. 458)

Indeed, it is challenging to find literature that refers to males observed in apparent total isolation from conspecifics (Mullins et al. 1988). Those studies on males (Best 1979, Christal and Whitehead 1997, Gaskin 1970, Goold 1999, Lettevall et al. 2002, Teloni et al. 2008), including some which concluded little or no apparent social organisation, still found pairs or larger clusters (i.e. synchronised clustering at the surface at close proximity). Others have identified ‘pairs’, or the same pair of males within minutes, for up to two hours (Christal and Whitehead 1997, Whitehead et al. 1992), or have defined “alone” as “The whale was alone: no whale was seen within ca. 1.5 h” (Weilgart and Whitehead 1988; p. 1935), and also referring to the presence of “males” (note plural) associated with hearing slow clicks (Weilgart and Whitehead 1988). Further evidence of possible strong bonds between males is the occurrence of several male-only stranding events (Clarke and Pascoe 1997, Mendes et al. 2007, Santos et al. 1999, Unger et al. 2016).

Similarly to slow click bouts in male-only foraging areas (Chapter 2, Jaquet et al. 2001, Oliveira et al. 2013), codas have also been associated with the ‘start’ and ‘end’ phase of foraging dives in female social units (Pavan et al. 2000, Teloni 2005, Watkins and Schevill

1977), in male bachelor groups in the Mediterranean Sea (Frantzis and Alexiadou 2008), and in the observation reported in Chapter 4). Even though there is no confirmation for the functionality of these diving-phase-related vocalisations, if their function is analogous between these observations, then the long-range properties of slow clicks (Madsen et al. 2002b) would likely cover a wider area than codas, which display lower sound levels and higher centre frequency (Chapter 4, Madsen et al. 2002a).

The frequency content of slow clicks (mean centre frequency of 3.2 kHz, Chapter 3) suggests that whales may use them to echolocate on large structures, such as the seafloor, conspecifics and bathymetric features (Goold 1999, Gordon 1987). My finding that the directionality of slow clicks (Chapter 3) may have further defined borders than previously suggested (Madsen et al. 2002b), and that slow clicking whales may be rotating on their longitudinal axis on their way to the surface, may indicate that, regardless of other possible functions, whales may use slow clicks for navigation in relation to large-scale bathymetry (Chapter 2). Similarly, slow click directionality may be used by the whales to obtain information on the distance, location and possibly individual features of other whales in their proximity, such as in the context of the observation of the pair of whales diving together (Chapter 4). Slow click echoes may additionally provide foraging cues to other sperm whales (Chapter 2).

Researchers agree that the function of slow clicks in breeding grounds is likely related to mating (Whitehead 2003), and that at high-latitude male-only feeding grounds their function must be a different one, given the absence of females (Oliveira et al. 2013). The groaning rates of male fallow deer (*Dama dama*) are higher when males are with females than when they are with other males, and males with females groan at higher rates when other vocal males are nearby (McElligott and Hayden 1999). The longer sequences of slow clicks reported in breeding grounds (Whitehead 1993) may follow a similar pattern as those found among the fallow deer. Moreover, if males adjust the beam direction of slow clicks by changing their body orientation (Chapter 3), this could aid individuals to reinforce their intentions by directing slow clicks to females, or to other males (both in breeding and feeding grounds), depending on the intentional context.

6.1. *Future research*

There is still a considerable lack of data on slow click patterns, both in male-only feeding grounds and at breeding grounds, due to the challenging and costly nature of collecting these

data. During my research I did not look at the slow click vocal repertoire of individuals. The possibility that inter-click interval (ICI) of slow clicks may reveal patterns should be investigated and compared between different individuals and geographical areas. Additionally, a detailed comparative analysis of slow click patterns, from complete dive cycles, between males at breeding areas and in male-only grounds, is needed to understand more fully how context may affect the outcome of these vocalisations.

To date, slow click studies in male-only foraging grounds have been restricted either to canyons (This study, Jaquet et al. 2001, Madsen et al. 2002b, Oliveira et al. 2013) or continental slopes (Mullins et al. 1988). Data on the acoustic behaviour of males foraging over the ocean basins, rather than over underwater canyons or continental slopes, but within high-latitude male grounds, could reveal additional information, particularly if slow clicks are used for echolocation (Chapter 2). Another valuable approach to further understand these clicks would be to design an experiment to expose sperm whales to recordings of slow click bouts, using different combinations of ICI and number and duration of bouts. This could potentially trigger vocal and/or behavioural responses from conspecifics.

Finally, my attempt of assessing a possible relationship between the multi-pulsed structure of slow clicks and the total body length of individuals (Chapter 3) should be repeated with a larger sample size, ideally with whales that differ markedly in body length. In addition, the nature of a multi-pulsed structure is unique to sperm whales (Norris and Harvey 1972), and it is a product of an echo from the initial sound pulse within the nasal complex sound-producing organ of this species (Møhl et al. 2003). The multi-pulsed structure found in slow clicks may thus result from the initial sound pulse following a different path inside the nasal complex (as opposed to that of other click types), which may involve a different equation relating the observed pulses with the total size of the animal, or the sound complex itself.

In conclusion, the regular use of slow clicks in this male feeding ground seems to suggest an important function associated with foraging at male-only grounds. Slow clicks appear to provide various types of information to other whales (Chapter 2, 3 and 4). However, the precise nature of that information is challenging to reveal. The slow click beam pattern, and the possibility that whales may target specific directions during bouts of slow clicks (Chapter 3), opens an additional and valuable research direction. This, coupled with other slow click-related information, may contribute to finally understanding the function, or possible multiple functions of slow clicks in different biological contexts.

6.2. References

- Au, W. W. 1993. The sonar of dolphins. Springer, New York.
- Beauchamp, G. 2005. Does group foraging promote efficient exploitation of resources? *Oikos* **111**(2):403-407.
- Beecher, M. D. 1989. Signalling systems for individual recognition: an information theory approach. *Animal Behaviour* **38**(2):248-261.
- Best, P. B. 1970. The sperm whale (*Physeter catodon*) off the west coast of South Africa. 5. Age, growth and mortality. Investigational Reports of the Division of Sea Fisheries, Department of Commerce and Industries, South Africa.
- Best, P. B. 1979. Social organization in sperm whales, *Physeter macrocephalus*. Pages 227-289 in H. E. Winn and B. L. Olla, editors. Behavior of Marine Animals. Springer US.
- Brown, J. L., and G. H. Orians. 1970. Spacing patterns in mobile animals. Annual review of ecology and systematics **1**:239-262.
- Bruck, J. N. 2013. Decades-long social memory in bottlenose dolphins. Proceedings of the Royal Society of London B: Biological Sciences **280**(1768):20131726.
- Christal, J., and H. Whitehead. 1997. Aggregations of mature male sperm whales on the Galápagos Islands breeding ground. *Marine Mammal Science* **13**(1):59-69.
- Clarke, M. R., and P. L. Pascoe. 1997. Cephalopod species in the diet of a sperm whale (*Physeter catodon*) stranded at Penzance, Cornwall. Journal of the Marine Biological Association of the UK **77**(4):1255-1258.
- Clarke, R. 1956. Sperm whales of the Azores. Discovery Reports XXVIII:237-298.
- De Leo, F. C., C. R. Smith, A. A. Rowden, D. A. Bowden, and M. R. Clark. 2010. Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. Proceedings of the Royal Society of London B: Biological Sciences **277**(1695):2783-2792.
- Fais, A., N. Aguilar de Soto, M. P. Johnson, C. Pérez-González, P. J. O. Miller, and P. T. Madsen. 2015. Sperm whale echolocation behaviour reveals a directed, prior-based search strategy informed by prey distribution. Behavioral Ecology and Sociobiology **69**(4):663-674.
- Frantzis, A., and P. Alexiadou. 2008. Male sperm whale (*Physeter macrocephalus*) coda production and coda-type usage depend on the presence of conspecifics and the behavioural context. Canadian Journal of Zoology **86**(1):62-75.
- Gaskin, D. E. 1970. Composition of schools of sperm whales *Physeter catodon* Linn. east of New Zealand. New Zealand Journal of Marine and Freshwater Research **4**(4):456-471.
- Gero, S., J. C. D. Gordon, and H. Whitehead. 2015. Individualized social preferences and long-term social fidelity between social units of sperm whales. *Animal Behaviour* **102**:15-23.
- Gero, S., H. Whitehead, and L. Rendell. 2016. Individual, unit and vocal clan level identity cues in sperm whale codas. Royal Society Open Science **3**(1):150372.

- Goold, J. C. 1999. Behavioural and acoustic observations of sperm whales in Scapa Flow, Orkney Islands. *Journal of the Marine Biological Association of the UK* **79**(3):541-550.
- Gordon, J. C. D. 1987. Sperm whale groups and social behaviour observed off Sri Lanka. PhD thesis. University of Cambridge, Cambridge, England.
- Herman, L. M., A. A. Pack, and M. Hoffmann-Kuhnt. 1998. Seeing through sound: dolphins (*Tursiops truncatus*) perceive the spatial structure of objects through echolocation. *Journal of Comparative Psychology* **112**(3):292-305.
- Jaquet, N., S. Dawson, and L. Douglas. 2001. Vocal behaviour of male sperm whales: why do they click? *Journal of the Acoustical Society of America* **109**(5):2254-2259.
- Jaquet, N., S. Dawson, and E. Slooten. 2000. Seasonal distribution and diving behaviour of male sperm whales off Kaikoura: foraging implications. *Canadian Journal of Zoology* **78**(3):407-419.
- Lamoni, L. U., R. Antunes, P. J. O. Miller, and P. L. Tyack. 2013. "Boy-talk": acoustic characterisation of sperm whale slow clicks in a male-only high latitude feeding ground. *International Bioacoustics Congress (IBAC)*, Pirenópolis, Brazil.
- Lettevall, E., C. Richter, N. Jaquet, E. Slooten, S. Dawson, H. Whitehead, J. Christal, and P. M. Howard. 2002. Social structure and residency in aggregations of male sperm whales. *Canadian Journal of Zoology* **80**(7):1189-1196.
- Madsen, P. T., R. Payne, N. U. Kristiansen, M. Wahlberg, I. Kerr, and B. Møhl. 2002a. Sperm whale sound production studied with ultrasound time/depth-recording tags. *Journal of Experimental Biology* **205**(Pt13):1899-1906.
- Madsen, P. T., M. Wahlberg, and B. Møhl. 2002b. Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and communication. *Behavioral Ecology and Sociobiology* **53**(1):31-41.
- Matthews, J. N., L. Steiner, and J. C. D. Gordon. 2001. Mark-recapture analysis of sperm whale (*Physeter macrocephalus*) photo-ID data from the Azores (1987-1995). *Journal of Cetacean Research and Management* **3**(3):219-226.
- McComb, K., C. Moss, S. Sayialel, and L. Baker. 2000. Unusually extensive networks of vocal recognition in African elephants. *Animal Behaviour* **59**(6):1103-1109.
- McElligott, A. G., and T. J. Hayden. 1999. Context-related vocalization rates of fallow bucks, *Dama dama*. *Animal Behaviour* **58**(5):1095-1104.
- Mendes, S., N. Jason, R. J. Reid, A. F. Zuur, and G. J. Pierce. 2007. Stable carbon and nitrogen isotope ratio profiling of sperm whale teeth reveals ontogenetic movements and trophic ecology. *Oecologia* **151**(4):605-615.
- Møhl, B., M. Wahlberg, P. T. Madsen, A. Heerfordt, and A. Lund. 2003. The monopulsed nature of sperm whale clicks. *Journal of the Acoustical Society of America* **114**(2):1143-1154.
- Mullins, J., H. Whitehead, and L. S. Weilgart. 1988. Behaviour and vocalizations of two single sperm whales, *Physeter macrocephalus*, off Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences* **45**(10):1736-1743.

- Norris, K. S., and G. W. Harvey. 1972. A theory for the function of the spermaceti organ of the sperm whale (*Physeter catodon* L.). NASA Special Publication **262**:397-417.
- Ohsumi, S. 1971. Some investigations on the school structure of sperm whale. Tokyo.
- Oliveira, C., M. Wahlberg, M. Johnson, P. J. O. Miller, and P. T. Madsen. 2013. The function of male sperm whale slow clicks in a high latitude habitat: communication, echolocation, or prey debilitation? *Journal of the Acoustical Society of America* **133**(5):3135-3144.
- Pace, D. S., A. Miragliuolo, M. Mariani, C. Vivaldi, and B. Mussi. 2014. Sociality of sperm whale off Ischia Island (Tyrrhenian Sea, Italy). *Aquatic Conservation: Marine and Freshwater Ecosystems* **24**(S1):71-82.
- Pavan, G., T. J. Hayward, J. F. Borsani, M. Priano, M. Manghi, C. Fossati, and J. C. D. Gordon. 2000. Time patterns of sperm whale codas recorded in the Mediterranean Sea 1985-1996. *Journal of the Acoustical Society of America* **107**(6):3487-3495.
- Pinela, A. M., S. Qu  rouil, S. Magalh  es, M. A. Silva, R. Prieto, J. A. Matos, and R. S. Santos. 2009. Population genetics and social organization of the sperm whale (*Physeter macrocephalus*) in the Azores inferred by microsatellite analyses. *Canadian Journal of Zoology* **87**(9):802-813.
- Pyke, G. H. 1984. Optimal foraging theory: a critical review. *Annual review of ecology and systematics* **15**:523-575.
- Rendell, L. E., and H. Whitehead. 2003. Vocal clans in sperm whales (*Physeter macrocephalus*). *Proceedings of the Royal Society of London B: Biological Sciences* **270**(1512):225-231.
- Rice, D. W. 1989. Sperm whale, *Physeter macrocephalus* (Linnaeus, 1758). Pages 177-233 in S. H. Ridgway and R. Harrison, editors. *Handbook of Marine Mammals*. Academic Press, London, UK.
- Richardson, W. J., C. R. Greene Jr., C. I. Malme, and D. H. Thompson. 1995. *Marine mammals and noise*. Academic Press.
- Santos, M. B., G. J. Pierce, P. R. Boyle, R. J. Reid, H. M. Ross, I. A. P. Patterson, C. C. Kinze, S. Tougaard, R. Lick, U. Piatkowski, and V. Hernandez-Garcia. 1999. Stomach contents of sperm whales *Physeter macrocephalus* stranded in the North Sea 1990-1996. *Marine Ecology Progress Series* **183**:281-294.
- Schulz, T. M., H. Whitehead, S. Gero, and L. Rendell. 2008. Overlapping and matching of codas in vocal interactions between sperm whales: insights into communication function. *Animal Behaviour* **76**(6):1977-1988.
- Straley, J., G. Schorr, A. Thode, J. Calambokidis, C. Lunsford, E. Chenoweth, V. O. Connell, and R. Andrews. 2014. Depredating sperm whales in the Gulf of Alaska: local habitat use and long distance movements across putative population boundaries. *Endangered Species Research* **24**(2):125-135.
- Teloni, V. 2005. Patterns of sound production in diving sperm whales in the northwestern Mediterranean. *Marine Mammal Science* **21**(3):446-457.
- Teloni, V., M. P. Johnson, P. J. O. Miller, and P. T. Madsen. 2008. Shallow food for deep divers: dynamic foraging behavior of male sperm whales in a high latitude habitat. *Journal of Experimental Marine Biology and Ecology* **354**(1):119-131.

- Tormosov, D. D. 1975. Ecologo-physiological basis of different structures of sperm whale concentrations. *Morskie Mlekopitajushie* **2**:127-129.
- Tyack, P. L., and C. W. Clark. 2000. Communication and acoustic behavior of dolphins and whales. Pages 156-224 in W. W. L. Au, A. N. Popper, and R. R. Fay, editors. *Hearing by whales and dolphins*. Springer, New York.
- Unger, B., E. L. B. Rebolledo, R. Deaville, A. Gröne, L. L. IJsseldijk, M. F. Leopold, U. Siebert, J. Spitz, P. Wohlsein, and H. Herr. 2016. Large amounts of marine debris found in sperm whales stranded along the North Sea coast in early 2016. *Marine Pollution Bulletin* **112**(1):134-141.
- Van der Linde, M. 2010. Long-term monitoring of sperm whales in Kaikoura, New Zealand: data-management, abundance, and population dynamics. MSc thesis. University of Otago, Dunedin, New Zealand.
- Waluda, C. M., and G. J. Pierce. 1998. Temporal and spatial patterns in the distribution of squid *Loligo* spp. in United Kingdom waters. *South African Journal of Marine Science* **20**(1):323-336.
- Watkins, W. A., and W. E. Schevill. 1977. Sperm whale codas. *Journal of the Acoustical Society of America* **62**(6):1485-1490.
- Weilgart, L., H. Whitehead, and K. Payne. 1996. A colossal convergence. *American Scientist* **84**(3):278-287.
- Weilgart, L. S., and H. Whitehead. 1988. Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). *Canadian Journal of Zoology* **66**(9):1931-1937.
- Whitehead, H. 1993. The behaviour of mature male sperm whales on the Galápagos Islands breeding grounds. *Canadian Journal of Zoology* **71**(4):689-699.
- Whitehead, H. 1994. Delayed competitive breeding in roving males. *Journal of theoretical biology* **166**(2):127-133.
- Whitehead, H. 2003. *Sperm whales: social evolution in the ocean*. University of Chicago Press.
- Whitehead, H., R. Antunes, S. Gero, S. N. Wong, D. Engelhaupt, and L. Rendell. 2012. Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: why are they so different? *International Journal of Primatology* **33**(5):1142-1164.
- Whitehead, H., S. Brennan, and D. Grover. 1992. Distribution and behaviour of male sperm whales on the Scotian Shelf, Canada. *Canadian Journal of Zoology* **70**(5):912-918.
- Whitehead, H., S. Waters, and T. Lyrholm. 1991. Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. *Behavioral Ecology and Sociobiology* **29**(5):385-389.
- Wilkinson, G. S. 1992. Information transfer at evening bat colonies. *Animal Behaviour* **44**:501-518.

Appendix 1 - Summary of modelling details (see Chapter 2 for details)

Table 1 – Variables used, definitions and structure type

Variable Name	Description	Variable structure
index	Individual dive number	integer
LinkI_ac	Acoustic follow link number	integer
individual1	Whale being acoustically and visually tracked - focal whale	integer
SC_E_tot	N slow click events throughout a dive cycle	integer
Ow_no_Mean_Link	Mean N of other whales acoustically detected during each follow	number
silence_no	N times the tracked whale went silent during diving, based on fixed ICI threshold ($ICI > 3\text{ s}$ & $ICI < 30\text{ s}$)	integer
Depth	Depth at dive location of the tracked whale	integer
Slow_pauseRC	ICI between first click of dive as slow click and following regular click	number
RC_ICImean_10Fclicks	ICI mean for the first 10 regular clicks of the dive (based on 3 s fixed threshold)	number

Table 2 – Model names (numbers) and variables retained in the different analysis.

Model name	Model type	Explanatory variable	Rand. Intercept (1 individual1) + (1 LinkI_ac)	Model selection likelihood ratio test - anova()	p-value
1	lmer	RC_ICImean_10Fclicks	Depth	1	0.000313
2	lmer	RC_ICImean_10Fclicks	1 +		
3	lmer	Slow_pauseRC	Depth	3	0.06869
4	lmer	Slow_pauseRC	1+		
5	lmer	Slow_pauseRC	Depth	5	0.000249
6	lmer	Slow_pauseRC	1+		

Model Name	Model Type	Explanatory variable	Rand. Intercept (1 individual1) + (1 index) + (1 LinkI_ac)	Family	P value	AIC
7	glmer	SC_E_tot	Ow_no_Mean_Link + silence_no	Poisson	0.0436 (Ow_no_Mean_Link) 0.0514 (silence_no)	309.9

Model Name	Model Type	Explanatory variable	Rand. Intercept (1 index) + (1 LinkI_ac)	Family	P value	AIC
8	glmer	Canyon	SC_E_tot	binomial	0.4286	40.9